



Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity?



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ABSTRACT

Modification of natural ecosystems has threatened biodiversity worldwide, with forests suffering especially. Strategies aimed at mitigating such loss in forests often include enrichment of deadwood, a critical resource for many decomposer species. However, it remains unclear how deadwood can best be enriched to most effectively promote the diversity of saproxylic species. In this study, we investigated saproxylic beetle diversity in experimentally exposed deadwood logs of 13 different tree species across 30 forests in three regions of Germany. We tested whether gamma-diversity differs between tree species and whether the alpha-diversity within an individual log depended on whether logs were placed in unmanaged beech forests, managed beech forests, or managed conifer forests. We found significant differences in gamma- and alpha-diversity of saproxylic beetles among tree species, but the ranking of tree species differed between regions, suggesting differences in regional beetle species pools. Randomization tests aiming to identify how many and which deadwood logs would need to be exposed to best conserve saproxylic beetle diversity, showed that the overall diversity of beetles increased with the number of tree species exposed, due to turnover of beetle species between tree species. However, some species (e.g. *Carpinus*) and species combinations (e.g. *Carpinus-Picea*) reached exceptionally high beetle diversity. Alpha-diversity was higher in conifer than in beech forests, but did not differ between managed and unmanaged beech forests. Canopy cover above logs and average stand temperature strongly influenced alpha-diversity, suggesting that environmental conditions that may be affected by management act as habitat filters for species assemblages. We conclude that deadwood enrichment strategies would be most effective when combining particular tree species that support highest diversity.

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1. Introduction

Modification of natural ecosystems has caused a loss of biodiversity worldwide (Newbold et al., 2015). In forests, management has led to a quantitative decrease of several constituents of old-growth forests, such as large reductions in the amount of deadwood and in the numbers of ‘veterans’ i.e. very old trees. This holds particularly true if management has been very intensive (Bauhus et al., 2009; Lindenmayer et al., 2012). As a consequence, animal communities in managed forests may differ from those of unmanaged forests (Bengtsson et al., 2000; Lassaue et al., 2012). Deadwood is important for forest biodiversity: one quarter of all forest species are saproxylic, i.e. depend on deadwood (Speight, 1989; Stokland et al., 2012). The lack of deadwood in managed

forests has hence repeatedly been shown to decrease biodiversity (Lassaue et al., 2011; Müller and Büttler, 2010) and to change the functional composition of communities (Gossner et al., 2013b; Seibold et al., 2015b). As an example, in Germany, 27% of saproxylic species are threatened (Seibold et al., 2015b).

Several conservation strategies consequently focus on the enrichment of deadwood in forests (Hutto, 2006; Hyvarinen et al., 2006). One strategy is to cease production in forests. However, setting aside enough and sufficiently large areas of forest is difficult if not entirely impossible due to economic interests and needs. This particularly concerns densely populated areas with limited forest reserves such as Central Europe, where cessation of logging would potentially result in an increased import of wood from other regions, causing conservation problems in those regions. In addition, managed forests may need a long time before pre-management levels of deadwood will be reached, due to the low natural tree mortality of medium aged-stands that are typical for most managed forests (Holzwarth et al., 2013; Sebek et al.,

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2013) and due to rapid decomposition of most deciduous tree species (Pietsch et al., 2014). Another strategy to enrich deadwood is to use harvest operations to leave some of the crowns or stems in the forest. This is the strategy currently favored in several countries where large natural disturbances such as windthrow are rare or – as in the case of insect pest outbreaks and forest fire – are prevented by all means. However, this strategy is increasingly threatened due to the increasing demand for wood for energy production (Bouget et al., 2012). The amount of deadwood necessary to preserve the diversity of saproxylic species is still under discussion (Lassauze et al., 2011).

Several fundamental questions on the dependence of saproxylic beetles on deadwood are still open. One most basic question concerns the degree of specialization: Are they mostly generalists accepting a wide variety of host species, or do they resemble herbivores showing a similar degree of host specialization? Up to now, no reliable answer could have been given to this question.

Host specificity of saproxylic beetles has only rarely been studied, with inconclusive results. In boreal forests, studies on the occurrence patterns of threatened species suggested a great importance of particular tree species, e.g. from the genera *Populus*, *Picea* and *Pinus*, suggesting host specialization (Lindhe and Lindelöw, 2004; Tikkanen et al., 2007; Tikkanen et al., 2006). In contrast, studies on tree species preferences in boreal and temperate forests suggest a lower degree of specialization (Milberg et al., 2014; Toivanen and Kotiaho, 2010). A further common perception is that the importance of tree species identity for host choice of saproxylic species generally decreases with increasing wood decay, because of the convergence of physical and chemical properties. However, differences between broadleaved and coniferous trees are assumed to persist along the decomposition process (Stokland et al., 2012).

One potential limitation of most studies on host specialization of saproxylic species is that they are based on collections of existing deadwood pieces. Because managed temperate forests only contain a few tree species, the diversity of deadwood in these forests is very limited and hence the choice for beetles also very restricted. It is thus not possible to extrapolate beetle host range beyond the host species found in the forest. Furthermore, we know little about whether saproxylic species would accept a tree species that does not occur as a living tree in a particular forest, e.g. if they would also colonize deadwood from pine in a pure beech or oak stand. If saproxylic species are indeed very host-specific, then their diversity will be limited by deadwood species diversity and related to forest stand diversity and species composition.

In addition to host specificity, it is known that the abiotic and biotic environment affects the community of saproxylic species in a particular forest. Large differences in the composition of saproxylic communities among forests and regions have been shown (Gossner et al., 2013a; Müller et al., 2013; Müller and Gossner, 2010), but the causes for this, independent of the availability of deadwood variation, are largely unclear. (Micro-)Climatic variables, such as temperature (e.g. sun-exposed vs. shaded substrates), influence the development of insect species and may affect their diversity (Gough et al., 2015; Lindhe and Lindelöw, 2004; Lindhe et al., 2005; Müller et al., 2015a; Sverdrup-Thygeson and Ims, 2002).

In this study, we investigated saproxylic beetle communities colonizing the deadwood of logs of 13 different tree species across 30 forests in three regions of Germany using a large-scale experiment. About 1150 logs of >20 cm diameter were exposed. We were interested in whether saproxylic species diversity during the early successional stage of deadwood decomposition depends on tree species identity, or on forest management, i.e. management intensity (managed vs. unmanaged) and forest type (coniferous vs. broad-leaved), which reflects the management decision of selecting a particular tree species. We tested this at different spatial diversity scales; within and across region gamma-diversity, which combines log-scale alpha-diversity as well as species turnover between logs (only tree species identity) and log-scale alpha-diversity (tree species identity, management, region).

Furthermore we used forest stand-based temperature and subplot-based canopy cover to test for the influence of microclimate on saproxylic beetle diversity. We addressed the following questions:

- 1) Does alpha- and gamma-diversity of saproxylic beetles differ between tree species?
- 2) Is beetle diversity on tree species consistent between regions?
- 3) Which tree species and tree species combinations promote the highest diversity of saproxylic beetles?
- 4) Does alpha-diversity depend on forest management and microclimate?

2. Material and methods

2.1. Study regions

The experiment was conducted in the framework of the Biodiversity Exploratories Project (www.biodiversity-exploratories.de; Fischer et al., 2010) comprising three regions; the UNESCO Biosphere Reserve Schorfheide-Chorin (henceforth “SCH”) in the glacially formed lowlands in north-eastern Germany (52°47′25″–53°13′26″N/13°23′27″–14°08′53″E, about 1300 km² in size, 3–140 m a.s.l.), the National Park Hainich and surrounding area of the Hainich-Dün (henceforth “HAI”) in the hilly lands of central Germany (50°56′14″–51°22′43″N/10°10′24″–10°46′45″E, about 1560 km², 285–550 m a.s.l.) and the UNESCO Biosphere Reserve Schwäbische Alb (henceforth “ALB”) in the low mountain range in south-western Germany (48°20′28″–48°32′02″N/9°10′49″–09°35′54″E, about 420 km², 460–860 m a.s.l.). With an annual precipitation of about 520–580 mm, SCH is one of the driest parts of Germany and has a mean annual temperature of 8.0–8.5°C. Most of the region is covered by forests of pine *Pinus sylvestris* (39%), beech *Fagus sylvatica* (12%) and oak *Quercus petraea* (9%). HAI (6.5–8.0 °C; 500–800 mm) is one of the largest continuous forest areas in Germany and is dominated by broadleaf trees; conifers comprise only 12% of the forest (pine *Pinus sylvestris*; spruce *Picea abies*; larch *Larix decidua*). ALB (6.0–7.0 °C; 700–1000 mm) is a highly fragmented, mixed forest landscape dominated by beech *Fagus sylvatica* (46%) and spruce *Picea abies* (24%).

2.2. Deadwood experiment

The Biodiversity Exploratory Long-term Deadwood experiment (‘BELongDead’) was set up in 2009, in the framework of a long-term study on the relationships between land use, biodiversity and ecosystem processes (Fischer et al., 2010). In the study regions, nine (ALB), nine (SCH) and twelve (HAI) research plots (100 m × 100 m) were established, in total 30 plots. These were selected by a stratified random sampling design from a total of >300 candidate plots per region (for details see Appendix A1). The stratified random selection of plots was also used to reduce spatial autocorrelation problems. Each plot was in one of three differently managed forest types with different levels of management intensity: currently unmanaged beech forest stands, which were previously managed up to 20–70 years ago; managed beech forest stands; and managed conifer stands (spruce in HAI and ALB and pine in SCH). Three replicates of each forest management intensity in each region were studied, except in HAI, where three additional managed beech forests were investigated, separating between even-aged and uneven-aged management of beech forests. In this study, we only focused on two forest management decisions, i.e. not managing vs. management and tree species selection, i.e. beech vs. conifer-oriented management. Because no unmanaged conifer forests exist in the study regions, we combined these two decisions in one variable “forest management” with the three levels ‘unmanaged beech’, ‘managed beech’, ‘managed conifer’.

On each plot deadwood logs of 13 tree genera (henceforth “tree species” for simplicity) were exposed in three replicates (subplots). Tree

species included *Acer* sp., *Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Larix decidua* Mill., *Picea abies* (L.) H. Karst., *Pinus sylvestris* L., *Populus* sp., *Prunus avium* L., *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus* sp. and *Tilia* sp. All logs were approximately 4 m long and had a mean diameter of 31 ± 5.9 cm (SD). All logs were cut in winter 2008/2009 in the state of Thuringia (Germany) and then transported to each plot. The logs were placed in random order beside each other with a distance of ca. 1 m between logs. We carefully followed a protocol to minimize the potential bias by colonization of logs prior to translocation to the experimental sites (see Appendix A1). Each plot received three sets of all 13 tree species (subplots). Owing to limited supplies, a single *P. avium* log each was missing on 27 plots, a single *Acer* spp. on 2 and a single *Fagus sylvatica* on one of the 90 subplots, resulting in 1140 logs that were exposed in the forests. Two of the subplots were included in present study that had all species except for 14 of the 30 research plots, where only one of the two subplots had *P. avium* and two plots, where either only one *F. sylvatica* or only one *Acer* was exposed resulting in 764 logs included in this study ($14 \text{ plots} * 13 \text{ species} * 2 \text{ logs} = 364 \text{ logs}$, $16 \text{ plots} * 12 \text{ species} * 2 \text{ logs} + 16 \text{ plots} * 1 \text{ species} * 1 \text{ log} = 400 \text{ logs}$).

2.3. Saproxylic beetle sampling

Here we analyze data from the 1st (2010) to the 3rd year (2012) after logs were exposed in the forests. We used closed emergence traps (Appendix A1) to sample insects. These traps sample insects emerging from the logs over a full season. Traps were installed in March 2010 (first subplot) and March 2011 (second subplot). Sampling vials were emptied monthly until the end of October and samples were stored in 70% ethanol. In autumn traps were dismantled for the winter. The traps were moved 35 cm down the log every year. Specimens were sorted to order by student helpers and beetles were identified to species level by taxonomic specialists. Species were classified as saproxylic according to Seibold et al. (2015b). For analyzing the effects on threatened species we used the German Red List of Beetles (Supporting information; Schmidl and Büche, 2016), which follows the International Union for Conservation of Nature (IUCN) classification. We included all species of the categories critically endangered (CR), endangered (EN), vulnerable (VU) and near threatened (NT).

The first subplot was sampled in all years (2010 to 2012); the second subplot was sampled from 2011 to 2012. In total of 379 logs were sampled in 2010 and 764 logs from 2011 to 2012. Due to trap damage caused by mice, which allowed beetles to escape, data from some logs in 2012 had to be excluded from the analyses. Our final dataset consists of 379 logs in 2010 (100% of all sampled logs), 730 logs in 2011 (96%) and 637 logs in 2012 (83%).

2.4. Covariates

Because colonization and development of beetles might be affected by microclimatic conditions, we used the mean temperature per plot during the growing season (March–October 2009–2012) as a proxy for forest stand-based microclimatic conditions and the canopy cover above each subplot (20 m radius) as a proxy for subplot-based microclimatic conditions, as covariate (for details see Appendix A1).

Canopy cover was assessed by airborne LiDAR surveying, which was conducted over the three study regions by Milan GmbH in 2008 (HAI) and 2009 (ALB, SCH) during leaf-on conditions. We computed the forest canopy cover of each subplot in a 20 m circle around each subplot center at 2 m above ground (for details see Appendix A1).

We additionally tested for effects of forest stand-based deadwood volume using data from a deadwood inventory in 2012 (see Kahl and Bauhus, 2014). Deadwood volume ranged from 4 to 60 m^3ha^{-1} (mean 25 ± 3 SE).

2.5. Statistical methods

To analyze our data we used recently developed methods for sample size- and coverage-based rarefaction and extrapolation to be able to compare gamma-diversity for Hill-numbers ${}^0\text{D}$ (species richness), ${}^1\text{D}$ (Shannon diversity) and ${}^2\text{D}$ (Simpson diversity; Chao et al., 2014; Jost, 2006). This allows us to analyze the effects of rare and common species on diversity in a common framework. All analyses were performed in R 3.2.4 (R Core Team, 2016).

2.5.1. Gamma-diversity estimates

As raw data for diversity estimates we used the occurrence of beetle species over one year as a replicate, i.e. for every log and every year the number of individuals of a particular beetle species was summed up, resulting in abundances of beetle species per log per year. The number of samples for a given tree species (reference sample) was therefore the total number of logs of that species sampled in a particular year. Gamma-diversity was estimated for all regions together and separately for each region using the iNEXT function in the iNext package (Hsieh et al., 2014).

To obtain estimates of gamma-diversity for the 13 different tree species we used a framework published recently (Chao et al., 2014). This 'diversity accumulation curve' framework extends methods for rarefaction and extrapolation of species richness (species accumulation curve; Colwell et al., 2012). It a) provides estimators for inter- and extrapolation of higher order Hill numbers (Hill, 1973; Jost, 2006; see Appendix A2), b) allows estimation of sample completeness (Chao and Jost, 2012) and therefore sample coverage-based estimation and c) uses a bootstrapping method for constructing confidence intervals around Hill numbers (Colwell et al., 2012). This facilitates the comparison of multiple assemblages.

We estimated species diversity curves for Hill-numbers based on sample size and sample coverage. Coverage is defined as the proportion of the total number of individuals in an assemblage that belong to species represented in the sample (Chao et al., 2014). The reference sample size for sample size-based estimates was the number of logs sampled of a tree species in a particular year. At $q = 0$ (${}^0\text{D}$), rare and abundant species are weighted equally (species richness), at $q = 1$ (${}^1\text{D}$), species are weighted in proportion to their frequency in the sampled community and at $q = 2$ (${}^2\text{D}$) abundant species receive more weight relative to their frequency. Diversity of beetles emerging from the 13 different tree species was compared for a range of base sample sizes (BSS) and base sample coverages (BSC), to assess robustness of findings. In BSS samples are standardized on the basis of sample sizes and in BSC on the basis of sample completeness. If sample coverage differs strongly between different tree species, the diversity (BSS) of beetles might be underestimated on those tree species that have low sample coverage relative to the other tree species. In this case, it can be tested if estimates of diversity for the tree species change when diversity is standardized to common sample coverage (BSC). In the main manuscript we present (1) Chao's BSS (Chao et al., 2014), that is, the higher value of the minimum doubled reference sample size and the maximum reference sample size among tree species and (2) Chao's BSC (Chao et al., 2014), that is, the higher value of the minimum coverage for doubled reference sample size and the maximum reference coverage among tree species. For details see Appendix A2. Significant differences in gamma-diversity between tree species were judged by non-overlapping confidence intervals (Schenker and Gentleman, 2001).

We then estimated gamma-diversity of particular tree species combinations, to test the effects of exposing deadwood of particular combinations of tree species in a forest, for combinations of two, three, four up to all 13 tree species. To do so, we first randomly sampled a fixed number of log-years for each tree species based on the tree species with the lowest sample size using the sample function in the data.table package (Dowle et al., 2015). This was necessary to equalize sample size and thus sampling effort for each tree species in each tree species

combination. We then calculated the estimated beetle diversity at $BSS = 208$ for all tree species combinations. To test for effects of different tree species richness on the diversity of saproxylic beetles we compared the richness categories (single trees, twofold, threefold etc. combinations) by permutation tests using 1000 randomizations. Finally we ranked the tree species combinations according to their estimated species richness.

2.5.2. Alpha-diversity estimates

To analyze the drivers of saproxylic beetle communities at the log scale we also calculated three q -levels based on Hill numbers, 0D (species richness), 1D (exponential of Shannon's entropy) and 2D (inverse of Simpson's concentration) following Jost (2006), using the diversity function in the vegan package (Oksanen et al., 2016). Importantly, each log was treated as a replicate. We used the diversity per log and year as response variables. Independent variables were the fixed factors tree species, region, forest type and year of sampling, which is a proxy for decay progress and the continuous predictors canopy cover, temperature and deadwood amount. Additionally we tested for two-fold interactions between tree species and the other independent variables.

We applied the multimodel inference approach as proposed by Grueber et al. (2011). We first formulated a global mixed model including all fixed effects and the nested structure of data, subplot within plot, was considered in the random term. This was done using the lme function in the nlme package (Pinheiro et al., 2016). We used diagnostic plots to estimate model performance and transformed data when necessary (species richness was log transformed). All continuous variables were scaled to zero mean and unit variance. Using Akaike information criteria corrected for small sample size (AICc) we selected those models from all possible models with $\Delta AICc < 2$ (substantial support) and $\Delta AICc 2-7$ (some support) as suggested by Burnham et al. (2011) by using the get.models function implemented in the package MuMIn (Bartoń, 2016). The subset of models was then averaged using parameter estimate and Akaike weight of each model with the model.avg function of the package (Grueber et al., 2011). Akaike weight of each model provide another measure of the strength of evidence for each model and represent the ratio of delta AICc values for each model relative to the whole set of candidate models. It indicates the probability that the model is the best among the whole set of candidate models. The relative importance of each independent variable was assessed by calculating the cumulative Akaike weights of models containing a particular predictor.

To test for spatial autocorrelation of diversity measures within and among regions we used the correlog function in ncf package (Bjornstad, 2016) based on 1000 randomizations.

3. Results

3.1. Beetle emergence and overall diversity

In total we sampled 71,881 individuals of 426 saproxylic beetle species (${}^1D = 111$; ${}^2D = 60$) emerging from 764 tree logs between 2010 and 2012. Abundance and diversity was highest in SCH (24,234 Ind., ${}^0D = 333$; ${}^1D = 128$; ${}^2D = 77$), followed by HAI (29,019; 241; 72; 41) and ALB (18,628; 194; 58; 33). 28 species occurred exclusively in ALB, 42 in HAI and 134 in SCH. At Chao's base sample size (BSS) of 934 (double the number of log-years) diversity was also estimated to be highest in SCH (${}^0D = 377$; ${}^1D = 131$; ${}^2D = 78$) followed by HAI (256; 72; 42) and ALB (223; 59; 33). For a complete list of sampled species see Appendix A3.

Estimated overall sample coverage for the 1746 log-years was 0.994, which means that about 0.6% of the total individuals in the assemblage are likely to belong to undetected species. In the ALB, estimated sample coverage was 0.987 (542 log-years), in HAI 0.988 (737) and in SCH 0.989 (467).

The tree species with the lowest reference sample size was the cherry tree with 104 log-years and thus we used BSS of 208 log-years (ALB:

62; HAI: 90; SCH: 56) for comparisons among all trees species. The corresponding calculated Chao's base sample coverage was 0.954 (ALB: 0.931; HAI: 0.945; SCH: 0.921), which means that 4.6% (6.9%; 5.5%; 7.9%) of the total individuals in the assemblage belong to undetected species. For details see Appendix A2.

Sampled beetles comprised 209 individuals of 42 endangered species (categories EN, VU, NT). No critically endangered species (CR) were observed. We found more endangered species in SCH (127 individuals, 37 species), than HAI (64, 13) and ALB (18, 6). Of these 27 occurred exclusively in SCH, 3 in HAI and 1 in ALB.

3.2. Beetle gamma-diversity among tree species

Overall gamma-diversity based on BSS significantly differed between tree species, indicated by non-overlapping confidence intervals (Fig. 1). Beetle species richness ($q = 0$) was higher in *Carpinus* (262; CI 240, 283) and *Picea* (244; 225,262) than in *Populus* (193; 178, 207), *Fraxinus* (185; 168, 202) and *Pseudotsuga* (179; 165; 193). *Fagus* (220; 203, 237) was intermediate, with higher species richness than *Fraxinus* and *Pseudotsuga*, but lower diversity than *Carpinus*.

Sample coverage at Chao's BSS in *Tilia* was significantly lower than in the other tree species. For *Tilia*, it was estimated that 5.3% of the total individuals in the assemblage belong to undetected species, whereas the estimated mean of the other tree species was $3.4\% \pm 0.001SE$. When using base sample coverage (Chao's BSC: 0.956), gamma-diversity ($q = 0$) of *Tilia* (Mean: 250; Min: 222; Max: 278) was higher than the other tree species, except for *Carpinus* (232; 216; 247), *Picea* (228; 211; 244) and *Larix* (209; 193; 225) (Fig. A4-1). Thus, for *Tilia* the adjusted values based on BSC differed from those obtained with BSS. For the other tree species results remained consistent, independent of the diversity measure used (i.e. BSS, BSC) (Table A4-1).

Changing the weight of rare and abundant species greatly changed the ranking of tree species, except *Carpinus* (${}^1D = 102$ species; ${}^2D = 60$) which remained the most beetle species diverse tree species. When increasing weighing of frequent species by increasing Hill numbers from 0D (species richness) to 2D (Shannon-diversity), the relative importance of *Picea* (${}^1D = 86$, ${}^2D = 44$) decreased from position 2 at 0D to position 11 at 1D to position 13 at 2D , indicating a steeper beetle rank-abundance curve for spruce, with many rare species, relative to the other tree species (Fig. A4-5). In contrast, *Pinus* (${}^1D = 89$; ${}^2D = 54$) increased from position 10 (0D) to 5 (1D) to 2 (2D). Also *Larix* (${}^1D = 86$; ${}^2D = 49$) and *Pseudotsuga* (${}^1D = 86$; ${}^2D = 49$) increased in their ranking from position 7 to 4 to 3 and 13 to 10 to 8, respectively. This shows that *Picea* is more important for rare species, whereas *Pinus*, *Larix* and *Pseudotsuga* are more important for common species. All other tree species, such as *Fagus*, did not show a consistent trend in their ranking (Figs. A4-2 & A4-3).

Threatened species showed similar among tree species patterns compared to all species, except for a higher importance of *Pinus* and lower importance of *Picea* (Fig. A4-4). Due to the low abundance and frequency of threatened species the confidence intervals were large and difference between species therefore not significant. *Fraxinus* was the only species that showed a significantly lower gamma-diversity of threatened species than the other tree species.

3.3. Effects of region on beetle gamma-diversity

When estimating gamma-diversity separately for each region, the ranking of tree species depended on the region (Fig. 1). However, *Carpinus* showed a consistently high species richness across regions (rank 1 in ALB and SCH; rank 2 in HAI). Estimated gamma-diversity of *Carpinus* was 1.4 times higher than that of the least beetle species-rich tree species (ALB: *Populus*; HAI: *Fraxinus*; SCH: *Pseudotsuga*). *Prunus* showed relatively higher species richness in HAI only (rank 1; ALB:12; SCH:9) and *Picea* in SCH (rank 2; ALB:5; HAI:6). The species richness of *Fraxinus* was relatively low in HAI (rank 13) and SCH (12), compared

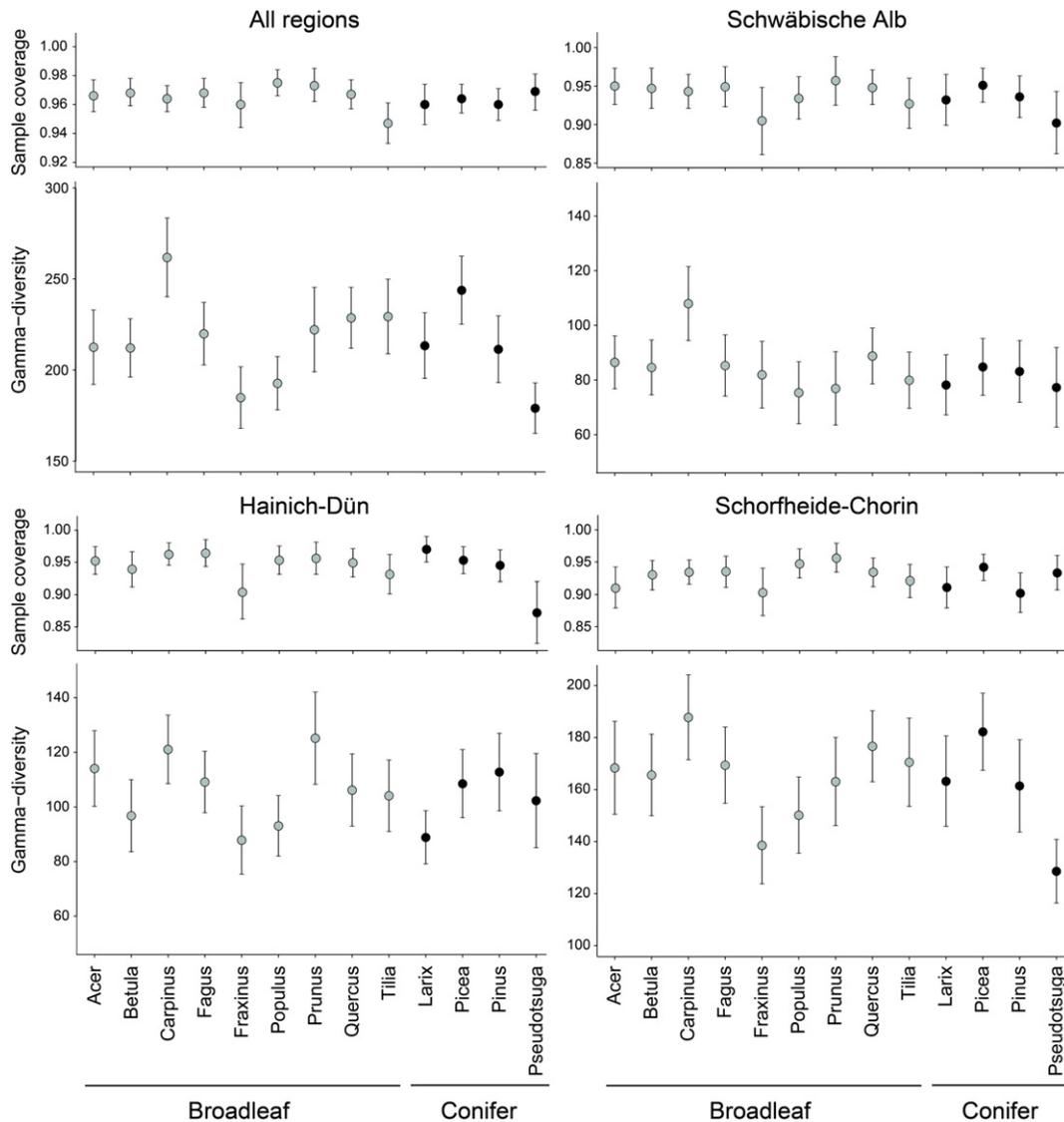


Fig. 1. Gamma-diversity ($q = 0$) of saproxylic beetle species sampled on 13 different tree species across three regions (All regions) and for each region separately (years 2010–2012 combined). Sample-based extrapolation to a total of 208 (Schw. Alb: 62; Hainich-Dün: 90; Schorfheide-Chorin: 56) log-years (double of the lowest sample size, i.e. *Prunus*) (bottom of each figure) and sample coverage at this base sample size (top of each figure) including 95% confidence intervals obtained by bootstrapping based on 200 replications. Please note different y-axis scales. Gray dots indicate broadleaf and black dots conifer trees.

to ALB (8), *Larix* in HAI (rank 12; ALB:10; SCH:8) and *Pseudotsuga* in SCH (rank 13; ALB:11; HAI:9). The regional distinction in *Pseudotsuga* was even more conspicuous in coverage-based estimates (13;1;1).

The ranking was only slightly modified when increasing the weighing of abundant species from 0D to 2D (Figs. A4-2 & A4-3). In all regions the rank of *Picea* decreased (ALB:5,10; HAI:6,12; SCH:2,6) while the rank of *Populus* in ALB (13,4), that of *Larix* in HAI (12,5) and that of *Pinus* in SCH (10,3) increased.

3.4. Beetle gamma-diversity for combinations of tree species

The more tree species combined, the higher the potential gamma-diversity that can be achieved, indicating species turnover among tree species (Fig. 2; for significant differences based on permutation tests see Table A5-1). However, a few single species and/or two- or three-species combinations showed a higher gamma-diversity than other tree species combination when total deadwood amount was kept constant. The combinations with the highest estimated number of species are shown in Fig. 2. *Carpinus* (only ALB) and combinations with *Carpinus* supported the highest species richness of beetles. Across regions and in ALB and SCH, *Picea* appeared to be the most effective additional species

in a mixture (in addition to *Carpinus*) to promote saproxylic species richness. In HAI, *Pinus*, *Fagus* and *Prunus* were more important than *Picea*. In SCH *Quercus* also contributed substantially to overall species richness, in addition to *Carpinus* and *Picea*. Overall these results suggest that combinations including *Carpinus* with either *Picea* or *Pinus* are most effective in promoting high beetle species richness.

When weighing abundant species more strongly by increasing Hill numbers, gamma-diversity still increased with increasing number of tree species combined (Figs. A5-1 & A5-2). Also the relative importance of *Carpinus* remained, except SCH, where *Quercus* (1D ; Fig. A5-1) and *Fagus* and *Tilia* (2D ; Fig. A5-2) increased in importance. Interestingly, also *Fraxinus* (overall and ALB) and *Pseudotsuga* (HAI) contributed more strongly to gamma-diversity when increasing q -levels. This shows that *Carpinus* especially contributes to the gamma-diversity of rare species while other tree species are equally or even more (in SCH) important in contributing to a high diversity of more abundant species. For a full list of tree species combinations and their gamma-diversity, see Table A5-2 to A5-5.

The importance of tree species and their combinations changed when focusing on threatened species. In particular, combinations of *Pinus*, *Tilia* and *Prunus* showed highest gamma-diversity (Fig. A5-3).

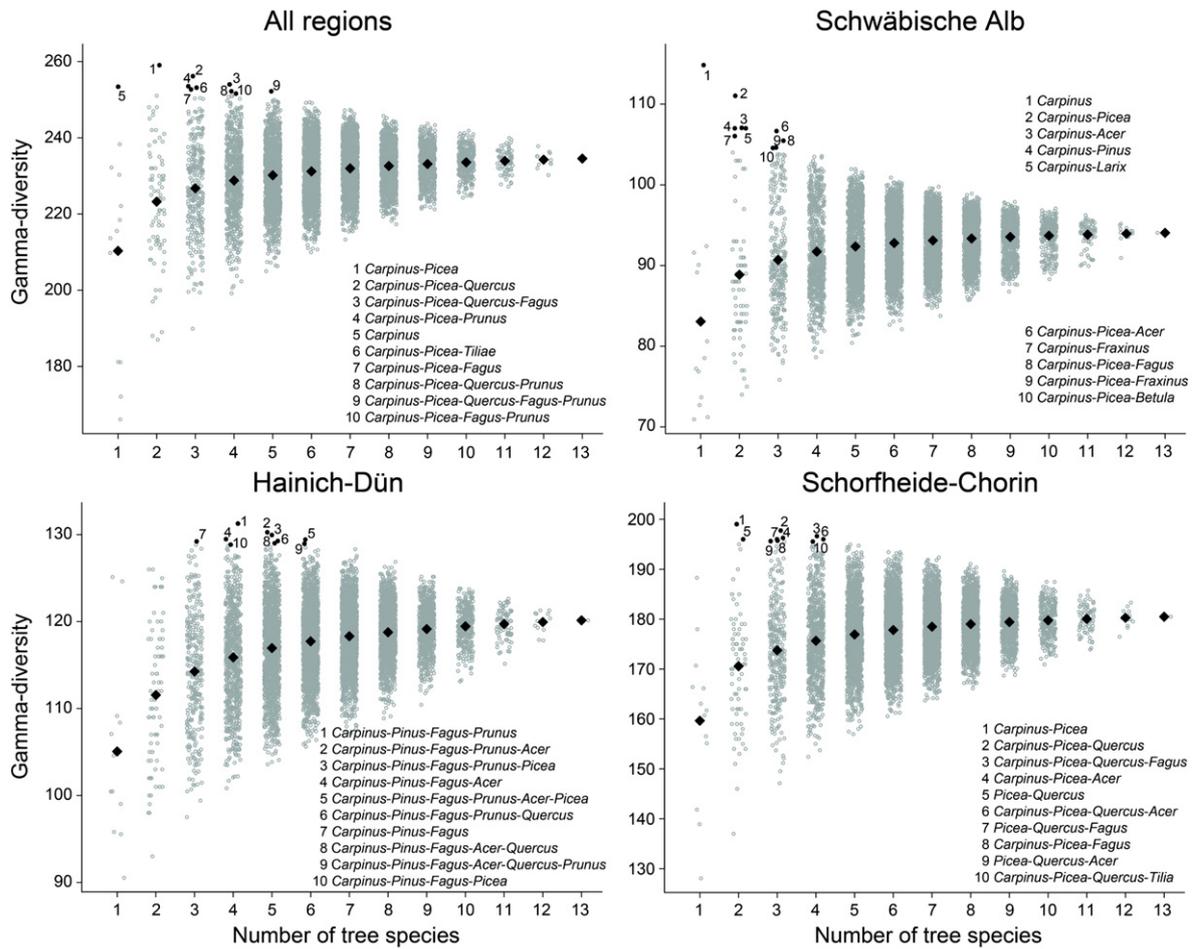


Fig. 2. Gamma-diversity ($q = 0$) of saproxylic beetles for the 13 different tree species and all twofold, threefold etc. tree species combinations across three regions (All regions) and for each region separately (years 2010–2012 combined). Sample-based extrapolation to a total of 208 (Schw. Alb: 62; Hainich-Dün: 90; Schorfheide-Chorin: 56) log-years. For each tree species we sampled randomly the number of logs that was available for the tree species with the lowest sample size (i.e. *Prunus*) prior to analyses and combined the same number of log-years for each tree species in tree species combinations. The black diamonds show the means per tree species richness. The ten tree species combinations with the highest estimated gamma-diversity are indicated by numbered black dots. For a full list of tree species combinations and their gamma-diversity, see Tables A5-2 to A5-5.

Confidence intervals were, however, large and overlapping (Table A5-6) and thus do not allow for a final conclusion.

3.5. Effects of region, management and climate on beetle alpha-diversity

The most important predictors of alpha-diversity (all q -levels and threatened species) at the log scale were year since harvesting, forest management, region and tree species (highest importance after model averaging; Table 1).

Alpha-diversity was higher in SCH than in HAI and ALB, for all q -levels (Figs. 3, A6-1 to A6-3). Diversity measures were spatially autocorrelated, positively within regions and between HAI and SCH and negatively between ALB and HAI/SCH, suggesting differences in local beetle species pools in ALB and HAI/SCH (Fig. A6-4). We found a higher diversity in conifer compared to beech forests when focusing on all species (0D , 1D), but decreasing richness of threatened species from unmanaged beech to managed conifer forests (Table 1, Figs. A6-3, A6-5). This was observed for all studied tree species (no interaction tree species \times forest type, Table 1).

Among broadleaf trees, highest alpha-diversity was found in *Carpinus* (all q -levels, RL-species), among conifers in *Picea* (0D) and *Pinus* (1D , 2D , RL-species). *Fraxinus* (all q -levels, RL-species), *Pseudotsuga* (0D , RL-species) and *Picea* (2D , RL-species) showed lowest alpha-diversity (Figs. 3, A6-1 to A6-3). There was an interaction between tree species and region (0D , RL-species), with *Prunus* and *Acer* being higher in HAI than in ALB, all other tree species had higher

alpha-diversity in ALB than HAI (Figs. 3, A6-1, A6-2). This resulted in a changed ranking of tree species according to their alpha-diversity. While *Acer* had a much higher ranking in ALB and HAI (0D :3) than SCH (0D :10), *Prunus* had a higher ranking in SCH and HAI (0D :2; 1D :3) than in ALB (0D :6; 1D :8) and *Tilia* in SCH (0D :6; 1D :5) than HAI (0D :12; 1D :8) and ALB (0D :13; 1D :13).

There was also an interaction between tree species and collection year, for all q -levels (Table 1). While *Picea* and *Pinus* (latter only 0D) showed highest species richness in the first year, all other tree species showed highest diversity in the second year (Fig. 3). For 1D and 2D no difference between the first two years were observed for *Betula*, *Carpinus*, *Fagus*, *Quercus* and *Pinus* (Figs. A6-1 & A6-2). When abundant species were more strongly weighted (2D) some tree species, such as *Quercus*, *Fagus* and *Prunus*, even showed highest diversity in the third year (Fig. A6-2). The lower difference between minimum and maximum value of mean species richness in the third year (5.7 species) compared to the first (7.6) and second year (8.7) indicate that diversities of tree species might converge with time, although this was not observed for higher q -levels.

Additionally, temperature, canopy cover and deadwood volume explained a substantial part of the variation in observed alpha-diversity. Alpha-diversity was additionally affected by our covariates. Alpha-diversity increased with increasing forest stand-based temperature and it also increased when subplot-based canopy cover decreased. Surprisingly deadwood amount was negatively related to alpha-diversity (Table 1, Figs 4 & A6-6 to A6-8). These results were consistent,

Table 1
Relative importance (IMP) of the potential predictor variables on saproxylic beetle diversity after model averaging. Additionally the number of models ($\Delta AICc < 2; \Delta AICc < 7$) containing a particular variable is shown (N). Variables with a relative importance > 0.7 are considered good predictors for the target variable (bold).

Variable	Species richness (q = 0)			Shannon (q = 1)			Simpson (q = 2)			RI-species (q = 0)				
	$\Delta AICc < 2$		$\Delta AICc < 7$	$\Delta AICc < 2$		$\Delta AICc < 7$	$\Delta AICc < 2$		$\Delta AICc < 7$	$\Delta AICc < 2$		$\Delta AICc < 7$		
	IMP	N	N	IMP	N	N	IMP	N	N	IMP	N	N		
Collection year	1.00	7	10	1.00	8	15	1.00	9	0.93	33	1.00	4	1.00	20
Forest management type	1.00	7	10	1.00	8	11	0.91	5	0.51	18	1.00	4	0.85	13
Region	1.00	7	10	1.00	8	15	1.00	9	1.00	40	1.00	4	0.93	15
Tree species	1.00	7	10	1.00	8	15	1.00	9	1.00	40	1.00	4	1.00	20
Collection Year:tree species	1.00	7	10	1.00	8	15	1.00	6	0.58	17	-	-	0.06	4
Temperature	0.43	3	5	0.46	4	9	0.45	9	1.00	34	1.00	4	0.97	17
Deadwood volume	0.34	3	4	0.37	4	7	0.40	5	0.46	19	0.33	2	0.31	8
Canopy cover	0.32	3	4	0.51	4	10	0.55	7	0.77	23	1.00	4	1.00	20
Region:tree species	-	-	2	-	-	-	-	-	-	-	-	-	-	3
Temperature:tree species	-	-	-	-	-	3	0.02	9	0.91	24	1.00	4	0.97	17
Canopy cover:tree species	-	-	-	-	-	-	-	-	<0.01	1	0.47	2	0.49	10

independent of tree species, the weighting of rare and abundant species and whether all species or threatened species were analysed. For 2D and threatened species, however, a significant interaction between tree species and temperature was observed (Table 1, Fig. A6–9), i.e. while all tree species showed an increase in beetle diversity with increasing temperature, the slopes differed between tree species, with steepest increases observed in *Fagus* and *Prunus* and flattest in *Picea*.

There was no interaction between tree species and forest management. Thus, the species identity of the deadwood was more important than whether surrounding forest was beech or spruce dominated, for saproxylic beetle species richness. Forest management thus only affected diversity through its effect on climatic conditions, i.e. lower canopy cover in conifer compared to beech forests (LME; $F = 7.62$, $p = 0.01$).

4. Discussion

In total, we sampled 426 saproxylic beetle species emerging from logs of 13 different tree species during the first three years of wood decomposition. This corresponds to 30% of ca. 1400 saproxylic beetle species known from Germany (Seibold et al., 2015a). As 33% of all saproxylic beetle species, i.e. around 462 species, are described to colonize fresh deadwood (Schmidl and Bußler, 2004) and our estimated sampling coverage is $> 99\%$, we conclude that in our study the saproxylic beetle fauna was sampled in an appropriate way.

Our first finding is that both gamma-diversity across all sites and alpha-diversity at the individual log scale, of saproxylic beetles consistently differed among tree species, indicating host specialization. *Carpinus* was the tree species that, unexpectedly, supported the highest number of saproxylic beetle species, also of threatened species. The diversity a particular tree species supported was largely unaffected by the forest in which the logs were exposed, which is the second main finding of our study. In contrast, the ranking of tree species differed between regions, indicating regional differences in species pools. Our third finding is that a very high richness of saproxylic species can be supported when logs of a single suitable tree species, in particular *Carpinus*, or particular combinations of two or three tree species, especially *Carpinus* and a conifer, are exposed in a forest. This is despite the fact that the overall diversity of saproxylic beetles increased with the number of tree species exposed, due to the large differences between tree species in the diversity of beetles they support and the differences in overlap in beetle communities between tree species. Our fourth finding is that alpha-diversity at the log scale is affected by microclimatic conditions, i.e. subplot-based canopy cover and stand-based average temperature. Finally, our study also shows that the exact results depend on the type of diversity measure considered, due to different behaviors of rare and abundant species and common and threatened species. In the following, we will discuss these findings one by one.

4.1. Differences in diversity among tree species

Our results are in line with studies showing that species richness of herbivores on trees varies greatly among tree species (Brändle and Brandl, 2001) which also applies to saproxylic beetles (Müller et al., 2015b). *Carpinus* among broadleaf and *Picea* among conifers were the most beetle species rich tree genera, which is in contrast to expert knowledge compiled in text books, suggesting that *Quercus* and *Pinus* are most important for saproxylic beetle diversity (Müller et al., 2015b). We believe that this major difference between our and previous studies is due to (a) a bias in the literature, whereby previous attention was focused mainly on *Quercus* and *Pinus* and (b) low deadwood availability of many of the species included in our study, e.g. *Carpinus*, due to their low availability in current forests. The high diversity on *Carpinus* might at least partly be due to its high rate of decomposition, also shown by highest CO_2 -emissions among the studied tree species (Kahl et al., 2015). This might allow species of later successional stages to colonize the *Carpinus* wood relatively early (see also, Müller et al.,

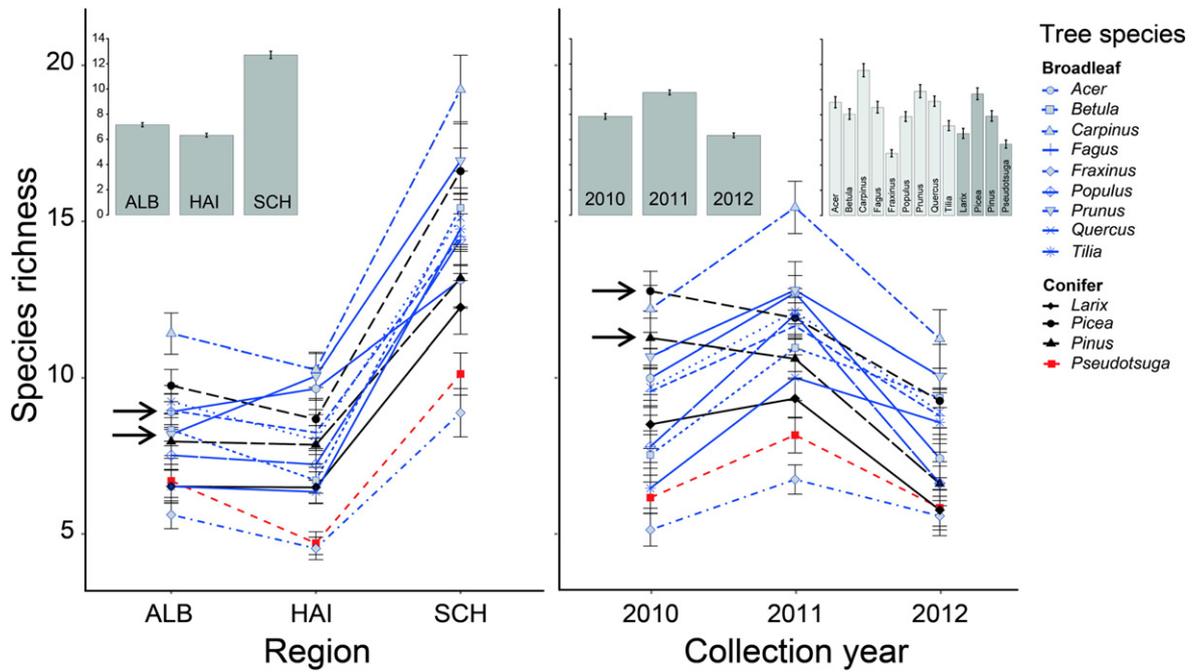


Fig. 3. Interaction plots showing effects of region and tree species (left) and year and tree species (right) on saproxylic beetle species richness ($q = 0$; shown as means \pm SE per log). Blue colors represent broadleaf. Black color native conifer and red color exotic conifer species. Arrows highlight tree species showing effects contrasting the main trend. Insets show main effects of region, year and tree species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2015b). A detailed analysis of the preferences of individual beetle species will be published elsewhere (Gossner et al., pers. comm.).

In contrast, *Fraxinus* and *Pseudotsuga* had overall low gamma- and alpha-diversity, particularly when giving strong weight to rare species (0D). *Fraxinus* is a member of the family *Oleaceae*, a phylogenetically isolated tree lineage within Central Europe, with a very specific chemical composition resulting in a herbivore community with low diversity and a high degree of specialization (Brändle and Brandl, 2001). *Pseudotsuga menziesii* was introduced to Europe from North America in the 18th century and is lacking an original insect fauna. Although adaptations of European insect species to *Pseudotsuga* have already been observed, the overall diversity, in particular of specialized species, is still lower compared to its natural range and to most native tree species

of Central Europe, partly explained by phylogenetic conservatism (Gossner et al., 2009; Roques et al., 2006). *Populus* was also comparably poor in species in our study. In other regions, such as Finland (Kouki et al., 2004), the UK (Rotheray et al., 2008) and Canada (Hammond et al., 2004) *Populus* is considered an important tree species for saproxylic insects, which emphasizes that the most effective tree species for saproxylic diversity conservation might differ between region, but further studies including a range of deadwood species are needed to conclude if this is really the case.

Our study shows that the differences between tree species persisted for the first three years after exposure. Early successional species with a one-year generation such as many bark beetles have been reported to use logs in the first few years (Raffa et al., 2015). Other species that

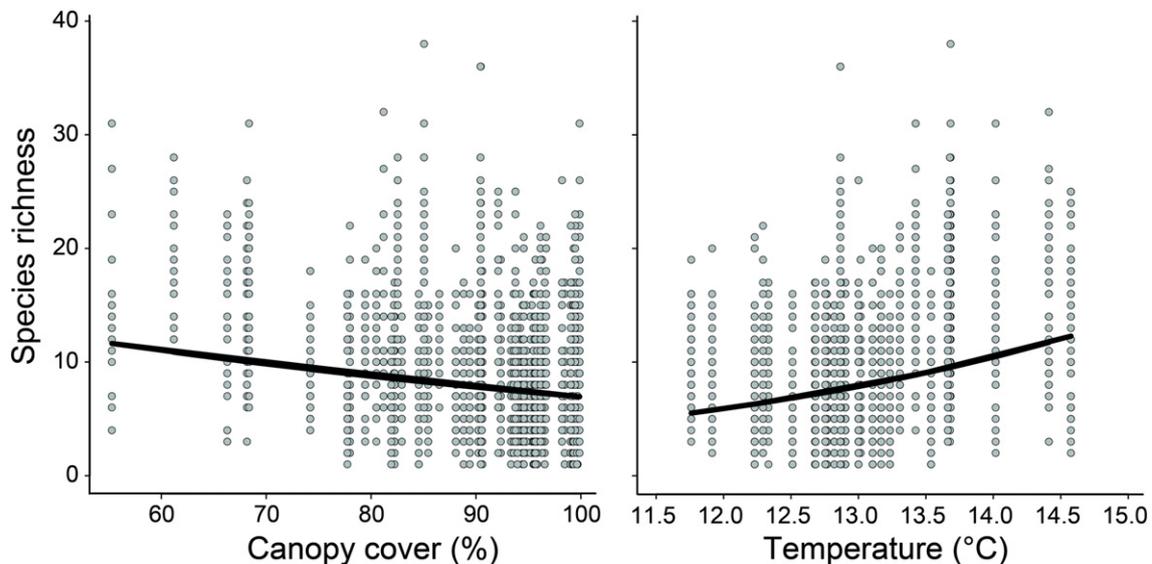


Fig. 4. Effect of canopy cover on subplot-level as proxy of microclimatic conditions (left) and temperature on forest stand-level (right) on saproxylic beetle species richness ($q = 0$). Regression lines show predictions from linear mixed effects models.

are abundant in early decay stages of logs need more than one year to complete larval development, such as many Cerambycids and therefore hatch only in the second or third year after exposure, even if they lay their eggs soon after tree death (Linsley, 1959). These two processes may be the reason why we observed the highest beetle species richness in the second year (third year after harvesting), for most tree species. Exceptions to this pattern were observed in *Picea* and *Pinus*, where diversity was highest in the first year, followed by a decrease in species richness. For conifer trees, a high overall proportion of fast-developing fresh-wood dwellers has been reported, in particular scolytids (Saint-Germain et al., 2007b). This difference to broadleaf trees has been proposed to result from differences in secondary chemistry, mechanical defense or the typical stand dynamics of tree species. Conifer stands are characterized by stand-replacing dynamics (windthrow, insect outbreaks) which provide periodically a large amount of freshly-killed trees and thus might have favored the evolution of stressed-host insect species.

4.2. Management effects

An important aim of the BELongDead experiment is to test the effect of forest management, i.e. unmanaged vs. managed forests and conifer vs. beech forests, on deadwood decay and diversity. We found significant differences between forest management types with highest overall diversity found in conifer forests, but highest threatened species richness in unmanaged forests. This suggests that forest abandonment in forest landscapes characterized by intensive management history does not promote overall diversity, but particular threatened species might profit. However, we found the same ranking of tree species with respect to their beetle diversity independent of whether the logs were placed in a beech forest or a pine or spruce forest. This suggests that beetle diversity was not affected by whether logs were in a stand of the same species or in a stand where the species did not occur. This suggests that saproxylic beetles of early decay succession have a very good host finding ability (Johansson et al., 2006; Ranius et al., 2011; Saint-Germain et al., 2007a). A caveat is that for the other species, in particular oak, we did not compare diversity of saproxylic beetles in oak logs in oak stands vs. other stands.

The most likely driver of the observed differences between broadleaf and conifer forests are differences in microclimatic condition between these forest types (see below). Deadwood pools of studied forest stands had only weak effects on beetle assemblage of exposed logs.

4.3. Regional differences

Gamma- as well as alpha-diversity was significantly higher in SCH compared to ALB and HAI. This and our analyses of spatial autocorrelation suggest different species pools in the three regions, which was largest in SCH, possibly due to favorable climatic conditions (Continental climate, warmest region during the growing season). SCH is also more species-rich in other arthropod guilds (Gossner et al., 2014). In addition, historic management may have shaped the saproxylic beetle species pool. In the SCH region forests have, for several centuries, been primarily managed to provide good hunting grounds for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), which probably allowed – in contrast to the other regions- for a higher proportion of post-mature trees and deadwood structures throughout the recent past. The almost exclusive occurrence of beetle species of primeval forests (Müller et al., 2005) in this region (ALB: 0 Ind.; HAI: 1 Ind.; SCH: 19 Ind./5 species; Table A3-1) might be an indication for this.

4.4. Importance of microclimate

We found a significant positive effect of forest stand temperature and a significant negative effect of canopy cover, on alpha-diversity of saproxylic beetles. Studies in northern Europe have shown that open,

sunny, early successional sites are particularly important for saproxylic (incl. beetle) diversity (Simila et al., 2002). Many oak specialists prefer sun-exposed deadwood, among these many endangered species (Franc and Gotmark, 2008; Ranius and Jansson, 2000), whereas *Carpinus* is a shade-tolerant species of the mid-story and thus associated communities might be adapted to shady conditions. Within the range of canopy cover observed (>55%), we did not find an indication for this as the diversity of both, *Carpinus* and *Quercus* increased with decreasing canopy cover in our study. We can, however, not exclude, that the ranking of tree species with respect to their beetle diversity might greatly change when stands become more open and deadwood sun-exposed; light demanding tree species such as oak and pine might become more important for beetle diversity under these conditions. Lindhe et al. (2005) for instance could show in Sweden that standing deadwood of light demanding oak and aspen supports a much higher proportion of species that show at least two-times higher densities in exposed compared to shaded substrate than less light-demanding spruce. Further experiments over the whole microclimatic range from open to shaded sites are needed to clarify this. However, forestry in Central Europe is increasingly developing uneven-aged beech forests during the last decades, which are characterized by rather shady conditions. Thus, our results are highly relevant for conservation strategies under current forestry conditions.

4.5. Tree species combinations and saproxylic species diversity

In our simulations, we investigated the effect of combining logs of an increasing number of tree species on expected diversity of saproxylic beetles. The relationship between gamma-diversity and the number of tree species combined was positive and saturating. Such saturating relationships between plant diversity and the species richness of various animal consumer groups (e.g. herbivores or predators) have also been found in experiments manipulating plant species richness in grasslands (up to 64 plant species, see Scherber et al., 2010). In contrast, previous non-experimental studies in Central European forests have found positive linear relationships between tree species diversity and the diversity of herbivorous beetles and true bugs (up to 11 tree species, see Sobek et al., 2009a; Sobek et al., 2009b). One possible explanation for this discrepancy are differences in the degree of specialization between herbivores and saproxylics: the fast saturation in species richness in our experiment with 13 tree species suggests that specialization in early successional saproxylic species is lower than in foliar herbivores. Alternatively, there may be confounding factors in descriptive studies that make it difficult to disentangle the effect of tree species richness from the effect of other factors on herbivore diversity (Schmid and Hector, 2004). Biodiversity experiments, in which tree species richness is manipulated as the independent variable will be able to test whether the relationship between tree diversity and herbivore diversity is linear or saturating (Bruehlheide et al., 2013).

Despite the overall increase in beetle gamma-diversity with the number of tree species combined in the simulations, particular two- and three-species combinations of tree species stood out that supported as much beetle diversity as more species combinations. These were combinations of *Carpinus* with some other species such as *Picea*. The combinations differed between the different regions, because individual tree species supported different saproxylic species diversity in different regions, except for *Carpinus* that showed consistently high diversity in all regions. Nevertheless, several two- and three-species combinations are able to support most of regional diversity of saproxylic species, including rare and common species (consistent for different q-levels). For threatened species *Pinus* seems to be more important than *Picea* in combination with broad-leaved tree species. It has to be considered, however, that some rare specialists depend on additional tree species, e.g. *Fraxinus*. In addition, the low number of individuals and species resulted in large confidence intervals and caution against strong conclusions for the threatened species.

In contrast, data from our experiment in the coming years will unravel the relationship between tree species diversity and gamma-diversity of later-successional species.

4.6. Implications for nature conservation

Early successional beetles are very important from a conservation and an ecosystem functioning perspective. Although many of these species are not threatened, e.g. most bark beetles, they form a large part of overall saproxylic diversity. In addition, they most likely affect later-successional species by building entrance ports for other species. Thus they can act as keystone species by creating habitats for species of conservation concern (Martikainen et al., 1999; Müller et al., 2008). Beside their own boring activity they promote wood decomposition by introducing fungi species (Hofstetter et al., 2015). Thus, a higher diversity of early successional species is likely supportive for ecosystem functions and for species of conservation concern.

Although standing deadwood is also of high importance for many saproxylic species, lying deadwood can be more easily enriched during regular harvesting activities. A main conclusion from our study on lying deadwood is that saproxylic species diversity can best be increased by delivering deadwood of particular tree species. Thus conservation strategies should not only focus on increasing deadwood amount –which is certainly important to support higher population densities of beetles–, but also on increasing deadwood quality (Similä et al., 2003), in our case tree species combinations that support diversity (e.g. *Carpinus* and *Picea*). Our results suggest that leaving individual logs of subdominant species in the forests may result in a higher conservation success of saproxylic species, than leaving larger amounts of dominant species, e.g. when this is beech. Comparative experimental studies in which either deadwood amount (by leaving deadwood of the dominant species in the forest) or logs of favorable tree species combinations are enriched will show if such a strategy can work in practice. Thereby it is crucial to consider that additional tree species can contribute to the diversity of rare and threatened species (e.g. *Pinus* in our study) and that regional differences due to different species pools as well as (micro-)climate conditions shape species assemblages.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.06.032>.

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References

Bartoň, K., 2016. Package ‘MuMIn’: multi-model inference. R-Package 1. 15, p. 6 (<https://CRAN.R-project.org/package=MuMIn>).

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258, 525–537.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manag.* 132, 39–50.

Bjornstad, O.N., 2016. ncf: spatial nonparametric covariance functions. R Package Version 1, pp. 1–7 (<https://CRAN.R-project.org/package=ncf>).

Böhme, J., 2005. Die Käfer Mitteleuropas, Band K-Katalog: Faunistische Übersicht. Elsevier GmbH, Spektrum Akademischer Verlag Heroldsberg.

Bouget, C., Lassaune, A., Jonsell, M., 2012. Effects of fuelwood harvesting on biodiversity – a review focused on the situation in Europe. *Can. J. For. Res.* 42, 1421–1432.

Brändle, M., Brandl, R., 2001. Species richness of insects and mites on trees: expanding Southwood. *J. Anim. Ecol.* 70, 491–504.

Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F., Chen, X.-Y., Ding, B., Durka, W., Erfmeier, A., Gutknecht, J.L.M., Guo, D., Guo, L.-D., Härdtle, W., He, J.-S., Klein, A.-M., Kühn, P., Liang, Y., Liu, X., Michalski, S., Niklaus, P.A., Pei, K., Scherer-Lorenzen, M., Scholten, T., Schuldt, A., Seidler, G., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wubet, T., Yang, X., Yu, M., Zhang, S., Zhou, H., Fischer, M., Ma, K., Schmid, B., 2013. Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods Ecol. Evol.* 5, 74–89.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J. Plant Ecol.* 5, 3–21.

Dowle, M., Srinivasan, A., Short, T., Lianoglou, S., 2015. data.table: Extension of Data.Frame. R Package Version 1.9.6. (<https://CRAN.R-project.org/package=data.table>).

Fischer, M., Bossdorf, O., Gockel, S., Hansel, F., Hemp, A., Hessenmoller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schoning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.D., Weisser, W.W., 2010. Implementing large-scale and long-term functional biodiversity research: the biodiversity exploratories. *Basic Appl. Ecol.* 11, 473–485.

Franc, N., Gotmark, F., 2008. Openness in management: Hands-off vs partial cutting in conservation forests, and the response of beetles. *Biol. Conserv.* 141, 2310–2321.

Gossner, M.M., Chao, A., Bailey, R.L., Prinzinger, A., 2009. Native fauna on exotic trees: phylogenetic conservatism and geographic contingency in two lineages of phytophages on two lineages of trees. *Am. Nat.* 173, 599–614.

Gossner, M.M., Floren, A., Weisser, W.W., Linsenmair, K.E., 2013a. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. *For. Ecol. Manag.* 302, 404–413.

Gossner, M.M., Lachat, T., Brunet, J., Isacson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., Mueller, J., 2013b. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conserv. Biol.* 27, 605–614.

Gossner, M.M., Fonseca, C.R., Pašalić, E., Türke, M., Lange, M., Weisser, W.W., 2014. Limitations to the use of arthropods as temperate forests indicators. *Biodivers. Conserv.* 23, 945–962.

Gough, L.A., Sverdrup-Thygeson, A., Milberg, P., Pilskog, H.E., Jansson, N., Jonsell, M., Birkmoer, T., 2015. Specialists in ancient trees are more affected by climate than generalists. *Ecol. Evol.* 5, 5632–5641.

Gruber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.

Hammond, H.J., Langor, D.W., Spence, J.R., 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Can. J. For. Res.* 34, 1–19.

Hill, M.O., 1973. Diversity and evenness – unifying notations and its consequences. *Ecology* 54, 427–432.

Hofstetter, R.W., Dinkins-Bookwalter, J., Davis, T.S., Klepzig, K.D., 2015. Chapter 6 – symbiotic associations of bark beetles. In: Vega, F.E., Hofstetter, R.W. (Eds.), *Bark Beetles*. Academic Press, San Diego, pp. 209–245.

Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *J. Ecol.* 101, 220–230.

Hsieh, T.C., Ma, K.H., Chao, A., 2014. iNEXT: iNterpolation and EXTrapolation for species diversity. R Package Version 2.0 (URL: <http://chao.stat.nthu.edu.tw/blog/software-download>).

Hutto, R.L., 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North America conifer forests. *Conserv. Biol.* 20, 984–993.

Hyvarinen, E., Kouki, J., Martikainen, P., 2006. Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conserv. Biol.* 20, 1711–1719.

Johansson, T., Olsson, J., Hjältén, J., Jonsson, B.G., Ericson, L., 2006. Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden. *For. Ecol. Manag.* 237, 335–341.

Jost, L., 2006. Entropy and diversity. *Oikos* 113, 363–375.

Kahl, T., Bauhus, J., 2014. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. *Nat. Conserv.* 7, 15–27.

Kahl, T., Baber, K., Otto, P., Wirth, C., Bauhus, J., 2015. Drivers of CO₂ emission rates from dead wood logs of 13 tree species in the initial decomposition phase. *For. Ecol. M.* 6, 2484.

Kouki, J., Arnold, K., Martikainen, P., 2004. Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. *J. Nat. Conserv.* 12, 41–52.

Lassaune, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11, 1027–1039.

Lassaune, A., Lieutier, F., Bouget, C., 2012. Woodfuel harvesting and biodiversity conservation in temperate forests: effects of logging residue characteristics on saproxylic beetle assemblages. *Biol. Conserv.* 147, 204–212.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. *Science* 338, 1305–1306.

- Lindhe, A., Lindelöw, Å., 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *For. Ecol. Manag.* 203, 1–20.
- Lindhe, A., Lindelöw, Å., Åsenblad, N., 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodivers. Conserv.* 14, 3033–3053.
- Linsley, E.G., 1959. Ecology of Cerambycidae. *Annu. Rev. Entomol.* 4, 99–138.
- Martikainen, P., Siitonen, J., Kaila, L., Punttila, P., Rauh, J., 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *For. Ecol. Manag.* 116, 233–245.
- Milberg, P., Bergman, K.-O., Johansson, H., Jansson, N., 2014. Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. *Insect Conserv. Divers.* 7, 508–522.
- Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. For. Res.* 129, 981–992.
- Müller, J., Gossner, M.M., 2010. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biol. Conserv.* 143, 625–633.
- Müller, J., Bußler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmid, J., Zabransky, P., 2005. Urwald relict species - saproxylic beetles indicating structural qualities and habitat tradition. *Waldökologie Online.* 2, pp. 106–113.
- Müller, J., Büssler, H., Gossner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodivers. Conserv.* 17, 2979–3001.
- Müller, J., Brunet, J., Brin, A., Bouget, C., Brustel, H., Büssler, H., Forster, B., Isacson, G., Köhler, F., Lachat, T., Gossner, M.M., 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. *Insect Conserv. Divers.* 6, 162–169.
- Müller, J., Brustel, H., Brin, A., Büssler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacson, G., Zapponi, L., Gossner, M.M., 2015a. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography* 38, 499–509.
- Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015b. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *J. Appl. Ecol.* 52, 753–762.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhussaini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2016. *vegan: community ecology package.* R Package Version. 2, p. 3 (<https://CRAN.R-project.org/package=vegan>).
- Pietsch, K.A., Ogle, K., Cornelissen, J.H.C., Cornwell, W.K., Bönisch, G., Craine, J.M., Jackson, B.G., Kattge, J., Peltzer, D.A., Penuelas, J., Reich, P.B., Wardle, D.A., Weedon, J.T., Wright, I.J., Zanne, A.E., Wirth, C., 2014. Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs. *Glob. Ecol. Biogeogr.* 23, 1046–1057.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., R Core Team, 2016. *nlme: Linear and Non-linear Mixed Effects Models.* R package version 3.1-125. (<URL: <http://CRAN.R-project.org/package=nlme>>).
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing, Version 3.2.4.* R Foundation for Statistical Computing, Vienna, Austria (URL <https://www.R-project.org/>).
- Raffa, K.F., Grégoire, J.-C., Staffan Lindgren, B., 2015. Chapter 1 - natural history and ecology of bark beetles. In: Hofstetter, R.W., Vega, F.E. (Eds.), *Bark Beetles.* Academic Press, San Diego, pp. 1–40.
- Ranius, T., Jansson, N., 2000. The influence of regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95, 85–94.
- Ranius, T., Martikainen, P., Kouki, J., 2011. Colonisation of ephemeral forest habitats by specialised species: beetles and bugs associated with recently dead aspen wood. *Biodivers. Conserv.* 20, 2903–2915.
- Roques, A., Auger-Rozenberg, M.-A., Boivin, S., 2006. A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. *Can. J. For. Res.* 36, 299–313.
- Rotheray, E.L., MacGowan, I., Rotheray, G.E., Sears, J., Elliott, A., 2008. The conservation requirements of an endangered hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae) in the British Isles. *J. Insect Conserv.* 13, 569–574.
- Saint-Germain, M., Buddle, C.M., Drapeau, P., 2007a. Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? *Agric. For. Entomol.* 9, 227–235.
- Saint-Germain, M., Drapeau, P., Buddle, C.M., 2007b. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. *Ecography* 30, 737–748.
- Schenker, N., Gentleman, J.F., 2001. On judging the significance of differences by examining the overlap between confidence intervals. *Am. Stat.* 55, 182–186.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M., Tschamtkke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468, 553–556.
- Schmid, B., Hector, A., 2004. The value of biodiversity experiments. *Basic Appl. Ecol.* 5, 535–542.
- Schmid, J., Büche, B., 2016. Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick. *Naturschutz und Biologische Vielfalt* 70 (in press).
- Schmid, J., Bußler, H., 2004. Ökologische Gilden xylobionter Käfer Deutschlands. *Nat. Schutz Landschaftplan.* 36, 202–218.
- Sebek, P., Altmann, J., Platek, M., Cizek, L., 2013. Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *Plos One* 8, e60456.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmid, J., Thorn, S., Müller, J., 2015a. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* 29, 382–390.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmid, J., Thorn, S., Müller, J., 2015b. Association of the extinction risk of saproxylic beetles and the ecological degradation of forests in Europe. *Conserv. Biol.* 29, 382–390.
- Simila, M., Kouki, J., Martikainen, P., Uotila, A., 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biol. Conserv.* 106, 19–27.
- Similä, M., Kouki, J., Martikainen, P., 2003. Saproxylic beetles in managed and seminatural scots pine forests: quality of dead wood matters. *For. Ecol. Manag.* 174, 365–381.
- Sobek, S., Gossner, M.M., Scherber, C., Steffan-Dewenter, I., Tschamtkke, T., 2009a. Tree diversity drives abundance and spatiotemporal beta-diversity of true bugs (Heteroptera). *Ecol. Entomol.* 34, 772–782.
- Sobek, S., Steffan-Dewenter, I., Scherber, C., Tschamtkke, T., 2009b. Spatiotemporal changes of beetle communities across a tree diversity gradient. *Divers. Distrib.* 15, 660–670.
- Speight, M.C.D., 1989. Saproxylic invertebrates and their conservation. *Council of Europe, Nature and Environment Series.* 42, pp. 1–79.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in Dead Wood.* Cambridge University Press, Cambridge.
- Sverdrup-Thygeson, A., Ims, R.A., 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol. Conserv.* 106, 347–357.
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Ann. Zool. Fenn.* 43, 373–383.
- Tikkanen, O.-P., Heinonen, T., Kouki, J., Matero, J., 2007. Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: cost-effective measures for multi-species conservation. *Biol. Conserv.* 140, 359–372.
- Toivanen, T., Kotiaho, J.S., 2010. The preferences of saproxylic beetle species for different dead wood types created in forest restoration treatments. *Can. J. For. Res.* 40, 445–464.