

Forest management and regional tree composition drive the host preference of saproxylic beetle communities

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Summary

1. Among saproxylic beetles, many early colonizers prefer particular host species. Ranking of preferred hosts of local saproxylic beetle communities is critical for effective dead-wood management in forests, but is rarely done because experiments with numerous tree species are labour and cost intensive.

2. We analysed the host preference of local saproxylic beetle communities on logs of 13 tree species in relation to management (unmanaged and managed beech stands, conifer plantations on natural beech sites) in three regions of Germany during the most critical period for host specificity, that is the first two years after harvesting. Hosts were ranked quantitatively based on the ordinal ranking of hosts by single beetle species, which in turn was based on the variation in beetle abundance. First, we employed a Bradley–Terry model in which ranking was derived from paired comparisons of host trees. Then, a model-based recursive partitioning of the Bradley–Terry model tested whether host preference of beetle communities is affected by stand management, region and decay progress of dead wood.

3. Our results indicated that beetle communities overall avoided logs of *Fraxinus*, *Pseudotsuga*, *Larix* and *Tilia*, and *Carpinus* ranked highest in preference. *Carpinus* also ranked highest for communities of broadleaf specialists; *Picea abies* ranked highest for communities of conifer specialists. Model-based recursive partitioning revealed that ranking of local hosts in conifer stands differed from that of broadleaf stands, and that ranking of hosts in broadleaf stands differed between regions, but only in the first year for both.

4. *Synthesis and applications.* Early-colonizing saproxylic beetle communities vary locally in their choice of host trees. Therefore, forest managers should focus on the enrichment of dead wood of regional tree species and tree species of the local stand to successfully promote early-colonizing beetle.

Key-words: biodiversity exploratories, colonization process, dead wood, ecosystem process, forest management, host species, saproxylic beetle, wood decomposition

Introduction

A main aim of conservation in managed landscapes is to identify critical resources, for example dung, carcasses or

natural dead wood, and to provide them to support local animal communities. However, this is difficult without knowledge of local variations in the preferences of assemblages for certain resources. It has, for instance, been shown that spatial changes in occurrence and phenology of the main and alternative host plants might influence

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the resource preference of herbivores (Nylén *et al.* 2009; Ostergard, Hambäck & Ehrlén 2009). Such environmentally triggered behavioural modifications at the species or community level should be known for conservation strategies aimed at effective provision of resources (Haisfield *et al.* 2010; Martínez-Abraín & Oro 2013).

In forests, approximately a quarter of all species depend on dead wood (Speight 1989). These saproxylic or wood-inhabiting species suffer from human use of wood resources, which has over millennia resulted in decreased quantities of natural dead wood in most forests (Seibold *et al.* 2014b). Today, a high number of saproxylic species, for example 27% of saproxylic beetles in Germany, are threatened (Seibold *et al.* 2014b), and various management strategies have been designed to increase the amount of dead wood (Hutto 2006; Hyvärinen, Kouki & Martikainen 2006).

The most rapid and realistic way to restore dead wood in most production forests is to actively enrich dead wood during logging operations (Seibold *et al.* 2014a). In contrast, if previously managed forests are set aside without further management, it will take many decades for pre-management levels of dead wood to accumulate because the natural tree mortality in medium-aged stands typical of production forests is low (Holzwarth *et al.* 2013; Sebek *et al.* 2013). When managers enrich dead wood for biodiversity conservation, they have to decide on the characteristics of the dead wood provided, that is which diameter, and whether snags or logs and in particular which tree species should be left. If the most dominant tree species of a region were to be used for dead-wood enrichment, this would lead, for example, to an increase of *Picea abies* dead wood throughout Europe's temperate zone as this species was in the past planted extensively there, outside its natural distribution range (Seibold *et al.* 2014b). Whether providing *Picea abies* dead wood can help to restore communities of saproxylic insects that normally occur in mixed natural forests is unknown; the role of host species is not well understood.

Similar to species that feed on leaves (Novotny & Basset 2005), saproxylic species show different degrees of host specificity, with a general trend of decreasing host specificity with advanced stages of decomposition (Speight 1989; Bussler *et al.* 2011). However, the real host specificity of saproxylic beetles and host preferences of local communities are unclear because host lists are based on non-systematic observations (e.g. Bense 1995 for Cerambycidae). Feeding experiments with saproxylic species, as with phylophagous species (see Novotny *et al.* 2010), are much more time-consuming (covering decades) and costly (logs are expensive to buy and to handle). It is unclear whether local communities of saproxylic species simply prefer the most dominant tree species in their immediate environment, as predicted by Brändle & Brandl (2001) and Bussler *et al.* (2011) based on host lists. If this is true, host preferences of saproxylic species in forests of different tree species composition and under different forest management should differ.

In this study, we used data from the first two years of an experiment in which logs of 13 different tree genera (henceforth referred to as tree species for simplicity; Figs 1 and 2) were exposed in forest stands subjected to one of three types of forest management, replicated in three different regions of Germany that vary in tree species composition. We quantitatively ranked the host tree species preferred by local saproxylic beetle communities; the tree species analysed included the current dominant species of the stand and species not occurring in the stand. We focused on the first two years because it is well documented in the literature that particularly beetles colonizing fresh dead wood or dying trees need to overcome chemical barriers (Wagner, Clancy & Lieutier 2002) and are much more host-related than those of later decomposition stages (Stokland, Siitonen & Jonsson 2012).

Specifically, we asked: (i) which host trees are preferred by saproxylic beetle communities, (ii) whether the choice of host trees by local saproxylic beetle communities is driven by local and regional resource availability or forest

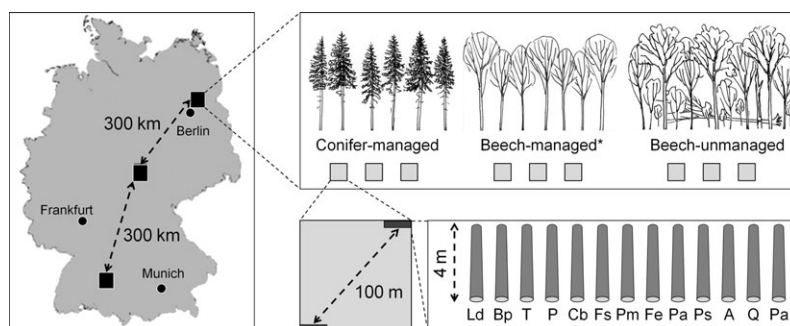


Fig. 1. Design of the BELongDead experiment. The experiment was conducted in three regions of Germany (A = Schwäbische Alb, H = Hainich-Dün, S = Schorfheide-Chorin). In each region, three forest types were studied with three site replications (* in Hainich-Dün, six managed beech forests were studied). Site replicates were randomly distributed within each region. Within each site, 13 logs of different tree species were exposed on each of two subplots in random order. Ld = *Larix decidua*, Bp = *Betula pendula*, T = *Tilia* sp., P = *Populus* sp., Cb = *Carpinus betulus*, Fs = *Fagus sylvatica*, Pm = *Pseudotsuga menziesii*, Fe = *Fraxinus excelsior*, Pa = *Picea abies*, Ps = *Pinus sylvestris*, A = *Acer* sp., Q = *Quercus* sp., Pa = *Prunus avium*.

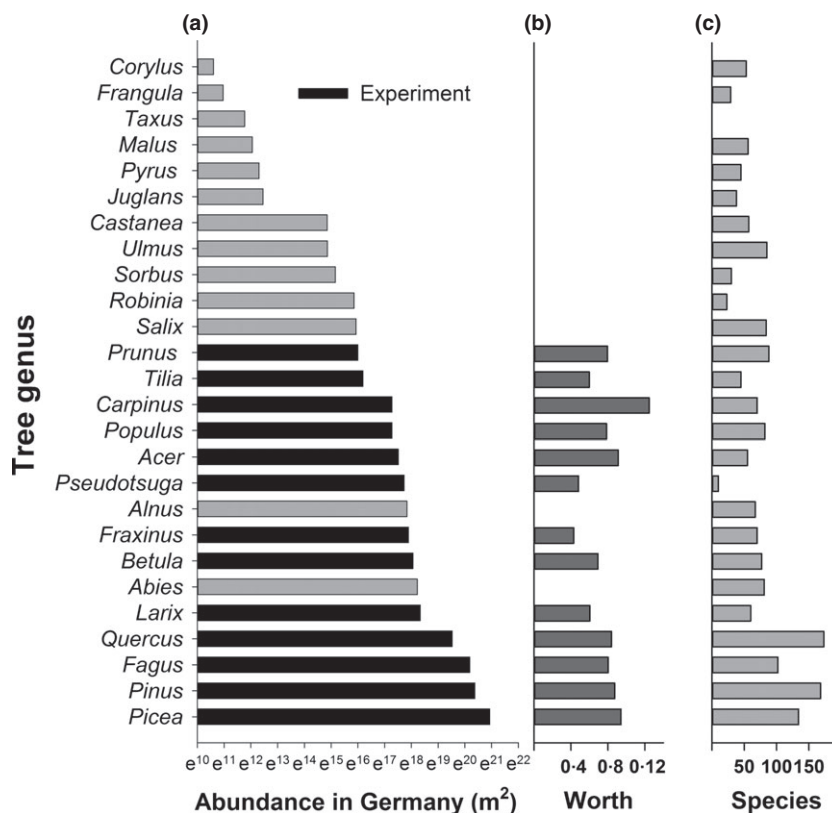


Fig. 2. (a) Abundance of the 26 most abundant tree species in Germany (data from the national forest inventory BWI2 from 2001). Logs of 13 tree species were exposed on each subplot of our long-term dead-wood experiment (black bars). (b) Overall worth parameter based on Bradley–Terry regression analysis, indicating the strength of the ranking of host preference of saproxylic beetle communities of each of 13 tree species, with higher values indicating higher ordinal ranks across beetle species. (c) Number of saproxylic beetle species reported from selected families according to Brändle & Brandl (2001) and Bussler *et al.* (2011).

management, (iii) whether host trees preferred by local saproxylic beetle communities change with the dead-wood decay progress, that is from the first to second year, and (iv) whether differences in host tree preference of local saproxylic beetle communities can be explained by differences in beetle species traits.

Materials and methods

The experiment was conducted in the framework of the Biodiversity Exploratories Project (www.biodiversity-exploratories.de; Fischer *et al.* 2010). The three study regions were the UNESCO Biosphere Reserve Schorfheide-Chorin in the glacially formed lowlands in north-eastern Germany, the National Park Hainich and surrounding area of the Hainich-Dün in the hilly lands of central Germany, and the UNESCO Biosphere Reserve Schwäbische Alb in the low mountain range in south-western Germany (Fig. 1). With an annual precipitation of about 520–580 mm, Schorfheide-Chorin is one of the driest parts of Germany. Most of the region is covered by forests of pine *Pinus sylvestris* (39%), beech *Fagus sylvatica* (12%), and oak *Quercus petraea* (9%). Hainich-Dün 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*). The Schwäbische Alb is a highly fragmented, mixed forest landscape dominated by beech *Fagus sylvatica* (46%) and spruce *Picea abies* (24%). For details, see Fischer *et al.* (2010).

EXPERIMENTAL DESIGN

In each study region, nine (Schwäbische Alb, Schorfheide-Chorin) or twelve (Hainich-Dün) research plots (100 × 100 m²) were

chosen (30 plots total). Each plot was in one of three differently managed forest types with different levels of management intensity (Fig. 1): unmanaged beech forest stands, which were previously managed up to 20–70 years ago in all study regions (score 1); managed beech forest stands (score 2); and planted conifer stands (score 3; spruce in Hainich-Dün and Schwäbische Alb and pine in Schorfheide-Chorin). Three replicates of each forest management type in each region were studied, except in Hainich-Dün, where three additional managed beech forests were investigated.

The long-term dead-wood experiment (BeLongDead) was set up in 2009. All logs were trunk parts of trees harvested within the extended Hainich-Dün region (Thuringia) in winter 2008/2009. All logs were exposed simultaneously in spring 2009 in the respective forest stands. Three sets (referred to as subplots hereafter) of fresh logs (length 4 m, diameter 20–60 cm), each with 13 different tree species of 13 different genera (*Acer* sp., *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Populus* sp., *Prunus avium*, *Pseudotsuga menziesii*, *Quercus* sp. and *Tilia* sp.) were placed on each research plot. For these genera, a phylogeny was estimated using a data assembly pipeline in R language (for details, see Bässler *et al.* 2014). We sampled two subplots per plot. The first subplot was sampled in both years (2010 and 2011); the second subplot was sampled only in 2011. In 13 of the 30 research plots, *Prunus avium* was exposed only in one of the two subplots due to limited log availability.

BEEBLE DATA

We used closed emergence traps to sample beetles emerging from the logs (for details, see Appendix S1, Supporting information). Traps were installed in March 2010 (first subplot) and March

2011 (second subplot). The traps of the first subplot were moved 35 cm down the log in the second year. Traps were emptied monthly until the end of October, and the samples were stored in 70% ethanol. Specimens were identified to the species level by taxonomic specialists and classified as saproxylic according to Seibold *et al.* (2014b). Traits of beetles were taken from recent published lists, including whether they were broadleaf or conifer specialists; body size, which correlates well with life-history traits; and niche position, that is canopy openness and decay progress (Gossner *et al.* 2013; Seibold *et al.* 2014b).

For the ranking of the preferred host tree species, we used the abundance of individual species emerging from each log of each subplot. We are aware that differences in the number of individuals emerging from each tree species can arise from various ecological processes. First, females of different species may differ in their host selection for ovipositioning and in the number of eggs laid in the selected host. Secondly, egg, larval, or pupal survival may differ between tree species. Owing to the sampling method, ranking of host preference of the local saproxylic beetle community based on ranking of host preference of single beetle species includes all these processes.

No data were available for 37 logs due either to the shortage of *Prunus avium* logs or to trap damage caused by animals, which allowed beetles to escape. Because we could not determine whether no beetles emerged or emerged beetles escaped through openings in damaged traps, all these 'zero' values were set to NA, that is data not available (Appendix S3, Supporting information).

RESOURCE AVAILABILITY

Resource availability, that is stock of each tree species, was estimated for each plot: (i) At the forest stand scale on five circular sampling inventory plots (radius 12.62 m) per each 1-ha plot (500 m² each; Schall & Ammer 2013). The minimum diameter at breast height of sampled trees was 7 cm (mean 33 ± 2 SE). The mean stem density per plot was 488 ± 81 SE trees per hectare; (ii) at the regional scale using data from the national forest inventory (BWI2 from 2001) for the two surrounding federal states (Bavaria and Baden-Württemberg for Schwäbische Alb, Thuringia and Hesse for Hainich-Dün, and Brandenburg and Mecklenburg-Vorpommern for Schorfheide-Chorin). For both sources, the proportion of the 13 target tree species was calculated based on the basal area of all trees inventoried and arcsine-square-root-transformed for further analyses.

STATISTICAL METHODS

All analyses were performed in R 3.0.2 (www.R-project.org); a detailed description of the methodological framework, including data and code, can be found in Appendices S2–5 (Supporting information). For calculating the ranking of host preference, we first calculated a ranking of host preference for each beetle species among the 13 logs of each subplot based on the decreasing number of emerged individuals. Note that the same tree species ranking for a single beetle species was estimated for a species with 1000/10/1 or 3/2/1 individuals in three species. With this approach, we fully considered beetle species identity across the plots and logs in contrast to simply determining species richness by counting beetle species on the logs. Moreover, we were able to exploit information on abundance variation of individual beetle

species. The ordinal ranking also allowed us to avoid an overestimation of the difference in the number of individuals, which can be high, particularly for species with a strong population dynamic.

To derive a 'consensus ranking' across individual beetle species for a particular community at the level of a subplot, we used the Bradley–Terry model (henceforth referred to as BT model; Bradley & Terry 1952). This model is used for deriving a ranking from paired comparison data when no natural measuring scale, for example an ordinal rank, is available (cf. Strobl, Wickelmaier & Zeileis 2011). This means that for each pair of 13 logs, that is 78 pairs total, we defined that a beetle species: (i) prefers the first tree species if its rank is higher, (ii) prefers the second tree species if its rank is higher or (iii) does not prefer one tree species over the other if both tree species have the same rank. The BT model allows us to estimate the probabilities for each of the three possible outcomes. To do so, a specific model parameter, the so-called worth parameter, in this case specific for tree species, is estimated for each tree species on each subplot (see, e.g. Strobl, Wickelmaier & Zeileis 2011). The worth parameter ranks the 13 host trees quantitatively from the highest value, that is most preferred host species, to the lowest value, that is least preferred host species, for a single beetle species on a subplot in a specific year. To obtain a baseline, we also computed one global BT model using the pairwise tree species rankings from all subplots as an estimate of overall host ranking or community host preference.

To separate the effect of local or regional abundance of a tree species from the effect of the tree species itself on the local rank order (worth parameter), we fitted again a linear mixed effects model with the worth parameter on each subplot per tree species and year as a dependent variable; tree species, year and their interaction as fixed effects; and stand and regional tree abundance as covariates. To account for the nested observation, we used a nested random factor of subplot, plot and region. The *P* values adjusted for multiple comparisons were calculated again using *glht*.

To test for variation in rank order determined by covariates, we used a recently developed model-based recursive partitioning approach for BT models (Strobl, Wickelmaier & Zeileis 2011; Eugster, Leisch & Strobl 2014). We were interested in testing whether local site covariates, decay stage of dead wood (using year as proxy), forest management type and region affect the ranking of host preference of beetle communities. Our model-based recursive partitioning procedure consisted of the following steps: (i) a BT model was fitted to the paired comparisons of all logs of one subplot of a specific year, (ii) the stability of the BT model parameters was assessed with respect to each available covariate, and (iii) if significant instability was detected, the sample was split along the covariate with the strongest instability, and the cut point with the highest improvement of the model fit was chosen in the final model. Steps i–iii were repeated recursively until there were no more significant instabilities. We applied this calculation to the full set of species in each community (Fig. 3), and to two subsets (conifer and broadleaf specialists). To test for possible bias owing to different sample sizes in 2010 and 2011, we repeated all tests and included only logs that were sampled in both years. We also tested for influence of rare species by restricting the analyses to species occurring in at least 10 samples. Neither test changed the results; thus, we only show results based on our full data set.

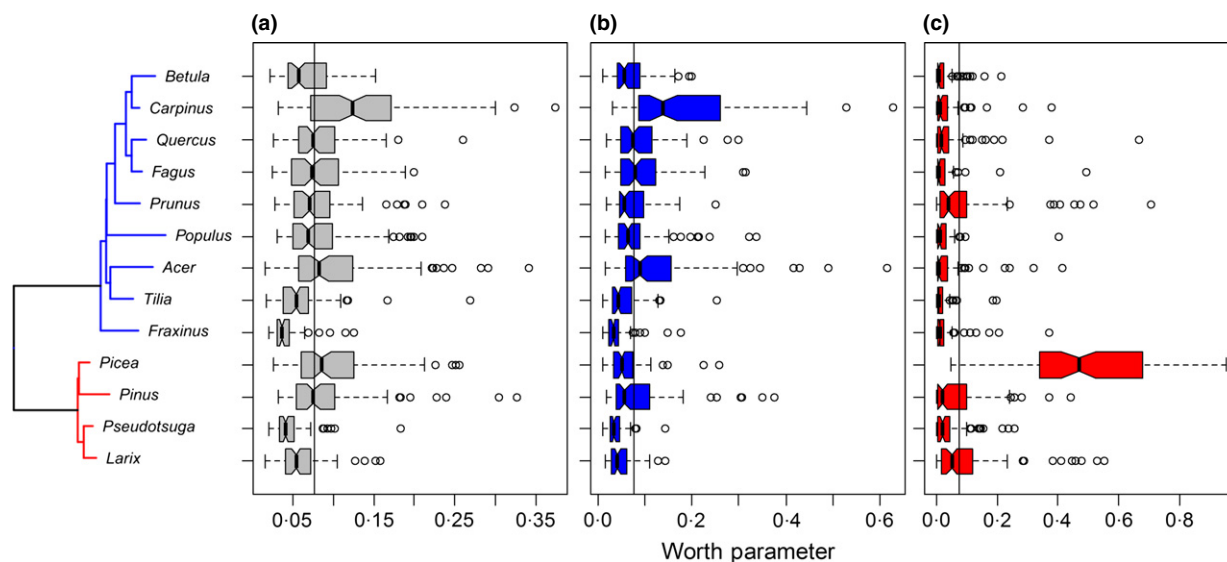


Fig. 3. Box and whisker plots of the worth parameter (higher values indicate higher ordinal ranks across beetle species) derived per subplot and year by the Bradley–Terry model for (a) all species, (b) broadleaf specialists and (c) conifer specialists. The phylogenetic tree (only genus names) is for illustrative purposes only. The vertical lines show the mean worth parameter over all subplots and years. Boxplots to the right of these lines indicate a rank of preference for this tree species by local beetle communities. Boxplots to the left of these lines indicate avoidance. Non-overlapping notches indicate significant difference, which were also supported by a post hoc comparison between tree species (not shown).

To ecologically characterize the groups of plots identified by recursive splitting, we compared the average trait values of the communities in each group using the above-mentioned traits, including host specificity (conifer specialist). This was done by hierarchical application of a generalized linear mixed effects model with a binomial error; the presence of a plot in a specific group was compared to all other plots, and the mean trait values were used as predictors for each split.

Results

A total of 57 134 individuals of 381 saproxylic beetle species of 52 families emerged from 378 logs (+13 NA) investigated in 2010 and from 725 logs (+24 NA) investigated in 2011. An analysis of all local worth parameters across the 13 tree species indicated that saproxylic beetles overall preferred logs of *Carpinus betulus* (indicated by significantly higher worth values compared to all other tree species, with $P < 0.01$ in a multiple post hoc test; Fig. 3a) and tended to avoid logs of *Fraxinus excelsior*, *Pseudotsuga menziesii*, *Larix decidua* and *Tilia* sp. (indicated by significantly lower worth values compared to most other tree species, with $P < 0.05$ in a multiple post hoc test and by non-overlapping notches with most others; Fig. 3a). This pattern was more pronounced when we restricted the analyses to either broadleaf or conifer specialists. Broadleaf specialists clearly only preferred *Carpinus betulus* and avoided conifer species, with the exception of *Pinus sylvestris* (Fig. 3b). Conifer specialists clearly preferred only *Picea abies* (Fig. 3c) and avoided all broadleaf trees, with the exception of *Prunus avium*. A generalized linear mixed effects model revealed a strong effect of tree species, but

no effect of resource availability at both the stand and regional scale on the worth parameter at the subplot level in 1 year (Table 1). The significant interaction of tree species and year for *Picea abies* indicated that the observed high rank of this tree species decreases over the two-first years of dead-wood decay. We found no phylogenetic signal in the worth parameter (function *phylosig* in package *phytools*, method = K, $P = 0.75$, see also Fig. 3).

Our recursive partitioning approach on the worth parameters revealed decay stage (year) of dead wood as a major factor affecting the ranking of host tree species (Fig. 4). In the second year (cluster E), variation in rank order could not be explained further by the covariates (Fig. 4). In contrast, within the first year, the rank order of coniferous stands (cluster A) and beech-dominated stands (managed and unmanaged) significantly differed. In the cluster of the coniferous stands, *Picea abies* and *Prunus avium* were the most-favoured species. The ranking in beech stands also differed among the three regions (clusters B, C, D). The mixed forest region Schwäbische Alb formed cluster B, with *Carpinus betulus* and *Picea abies* as the tree species with high rank values. Cluster C was formed by broadleaf stands in the broadleaf-dominated region of Hainich-Dün, with *Acer* sp., *Carpinus betulus* and *Fagus sylvatica* as the most preferred tree species; in the pine-dominated region Schorfheide-Chorin (cluster D), *Pinus sylvestris* was the highest ranked tree species.

Our post hoc characterization of saproxylic beetle communities in the five clusters showed that beetle communities in wood of advanced decay (2011; group E in Fig. 5) consisted of species that were less likely to be conifer

Table 1. Results of a generalized mixed effects model testing the effects of tree species, interaction of decay (year) and tree species, and resource availability at the stand and regional scales on the worth parameter. This parameter indicates the strength of the ranking of each of 13 tree species hosts preferred by saproxylic beetle communities. A nested factor for subplot in plot in region was applied for the replicated measures

Predictor	Estimate	SD	Z value	P value
Tree species				
<i>Fraxinus excelsior</i>	0.039	0.008	4.702	<0.001
<i>Pseudotsuga menziesii</i>	0.046	0.008	5.628	<0.001
<i>Tilia</i> sp.	0.052	0.008	6.422	<0.001
<i>Larix decidua</i>	0.064	0.008	7.613	<0.001
<i>Betula pendula</i>	0.055	0.008	6.603	<0.001
<i>Populus</i> sp.	0.062	0.008	7.61	<0.001
<i>Prunus avium</i>	0.100	0.009	10.552	<0.001
<i>Fagus sylvatica</i>	0.076	0.010	7.581	<0.001
<i>Quercus</i> sp.	0.076	0.008	8.567	<0.001
<i>Pinus sylvestris</i>	0.082	0.010	7.592	<0.001
<i>Picea abies</i>	0.130	0.011	11.912	<0.001
<i>Acer</i> sp.	0.089	0.008	10.708	<0.001
<i>Carpinus betulus</i>	0.127	0.008	15.541	<0.001
Resources				
Resource stand	0.001	0.006	0.166	1.000
Resource region	0.012	0.014	0.836	1.000
Tree species × year				
<i>Fraxinus excelsior</i> × 2011	0.001	0.010	0.148	1.000
<i>Pseudotsuga menziesii</i> × 2011	-0.001	0.010	-0.068	1.000
<i>Tilia</i> sp. × 2011	0.009	0.010	0.896	1.000
<i>Larix decidua</i> × 2011	-0.011	0.010	-1.096	0.999
<i>Betula pendula</i> × 2011	0.016	0.010	1.622	0.907
<i>Populus</i> sp. × 2011	0.026	0.010	2.685	0.159
<i>Prunus avium</i> × 2011	-0.029	0.012	-2.522	0.241
<i>Fagus sylvatica</i> × 2011	0.001	0.010	0.117	1.000
<i>Quercus</i> sp. × 2011	0.005	0.010	0.577	1.000
<i>Pinus sylvestris</i> × 2011	0.002	0.010	0.236	1.000
<i>Picea abies</i> × 2011	-0.055	0.010	-5.55	<0.001
<i>Acer</i> sp. × 2011	0.017	0.010	1.737	0.845
<i>Carpinus betulus</i> × 2011	0.010	0.010	1.000	1.000

specialists (lower proportion of conifer specialists); on average larger species; species of a later decomposition niche position and species with a niche position towards more shady forests. Cluster A (conifer vs. beech stands), and in the following also cluster B (Schwäbische Alb vs. Hainich-Dün/Schorfheide-Chorin), was split from the other groups due to higher proportions of conifer specialists (marginally significant; Fig. 4). Furthermore, saproxylic beetle communities in the beech forests of the Schorfheide-Chorin (cluster D) showed on average a niche position towards more open forests when compared to beetles in the beech forests of Hainich-Dün (marginally significant; Fig. 5).

Discussion

Our approach in which logs of 13 host tree species were simultaneously exposed in the field revealed the first

statistical evidence of host preference of saproxylic beetles obtained experimentally. More importantly, we could demonstrate that local saproxylic beetle communities differed in their tree host preference depending on the stage of the decay process (year), the type of stand (beech or conifer) and the region. Thus, our results not only increase the understanding of mechanisms underlying host selection by saproxylic beetles, but also provide new important implications for dead-wood management of forests beyond the amount (Lassauce *et al.* 2011).

Ever since Erwin (1982) used assumptions of host specificity to estimate global species richness, ecologists have improved methods to estimate host preferences. The 'effective specialization' (f_k) of arthropods on a host tree can be calculated by downweighting species with increasing sharing of different host tree species (May 1990). To predict the effective specialization for all host trees in a local forest, Ødegaard *et al.* (2000) expanded this approach to predictive models of general host specificity. In contrast to these approaches, we were mainly interested in a valid ranking of host species preferred by local beetle communities on a subplot; neglecting abundances would ignore important ecological information. Nevertheless, when we compared the effective specialization for each tree species on the subplots averaged across all subplots and compared this with the global worth parameter, we found a clear correlation ($\text{cor} = 0.62$, $P = 0.02$; Appendix S6, Supporting information). In a second, recent approach to identify preference of saproxylic beetles for hollow broadleaf trees as hosts, single beetle odds ratios were considered in a meta-analysis (Milberg *et al.* 2014). Such an approach is feasible, but again ignores abundances and is only applicable with host replications within one sampling unit. In contrast, our approach is more flexible because we can also analyse subplots without host replications and therefore can utilize the entire covariate information, such as forest management type, region and year. Our framework applied to host preference of beetle communities thus provides new opportunities for analyses considering abundance data using ordinal ranking. Ordinal ranking makes our approach more robust against both random variations in species abundances and rare species and simultaneously increases information about the community compared with presence-absence data. Moreover, the application of recursive partitioning of Bradley-Terry models allows us to test in a joint model framework whether host ranking depends on covariates.

Some of the observed positive or negative host rankings are to be expected. The generally avoided *Fraxinus excelsior*, an Oleaceae, is phylogenetically isolated within Central European tree genera (Fig. 3) and has a very specific chemical composition (Fig. 2c; Brändle & Brandl 2001), which allow only a few specialized saproxylic species to develop in its logs (see for longhorn beetles Bense 1995). The generally avoided conifer *Pseudotsuga menziesii* is not native to Central Europe and has been cultivated there for <200 years (Schmid, Pautasso & Holdenrieder 2013).

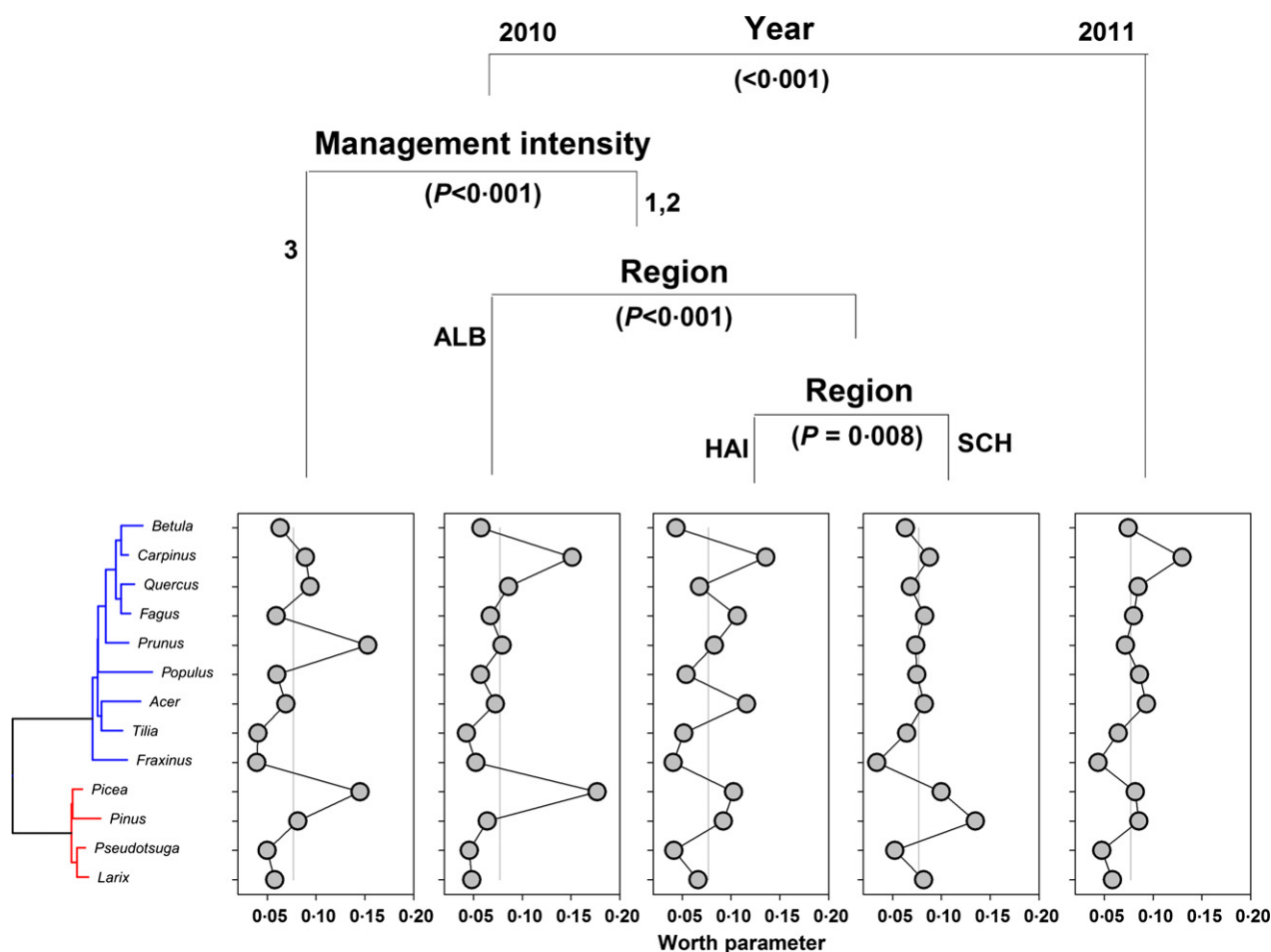


Fig. 4. Results of a recursive partitioning of Bradley–Terry models for all sampled saproxylic beetle communities. The worth parameter provides a ranking strength of the preference of saproxylic beetles for a specific tree species (higher values indicate higher ordinal ranks across beetle species). The vertical pale line indicates the mean worth value. The phylogenetic tree (only genus names) on the left is for illustrative purposes only. Management intensity: 1 = unmanaged beech forests, 2 = managed beech forests, 3 = managed conifer forests; region: ALB = Schwäbische Alb, HAI = Hainich-Dün, SCH = Schorfheide-Chorin. Letters A–E indicate the five clusters built by the tree.

This is in line with Buse *et al.* (2010), who found far lower numbers of saproxylic beetles in Israeli forests of the non-native conifer *Pinus brutia* than in native conifer stands. In contrast, a study restricted to scolytids colonizing experimentally exposed dead wood in France showed no difference in species numbers between native and non-native conifer species, including *Pseudotsuga menziesii* (Bertheau *et al.* 2009). The lower rank of *P. menziesii* found in our study might be due to a lower number of specialists. This is in keeping with a study of saproxylic canopy arthropods in southern Germany (Gossner & Ammer 2006) and also with a more pronounced lower value of the effective host specialization compared with the worth parameter on this conifer in our study (see Appendix S6). The observed low rankings of the hosts *Larix decidua* and *Tilia* sp. in our study can be explained by a generally lower number of herbivorous species, including saproxylic beetles, colonizing these tree species (Fig. 2c) and/or by the lower abundance of these trees in Germany compared with the related coniferous species

(*Pinus sylvestris* and *Picea abies*) and broadleaf species (Brändle & Brandl 2001).

The high preference of saproxylic beetle communities for *Picea abies* as host is probably due to its general attractiveness to most conifer specialists (Fig. 3) and its high resource availability in Germany (Brändle & Brandl 2001; Bussler *et al.* 2011). The more challenging question is why in particular broadleaf specialists preferred *Carpinus betulus* so strongly (Fig. 3); from this tree species, literature data suggest a relatively low number of phytophagous insects compared with other broadleaf tree species and its availability as a resource in Germany is low (Fig. 2c; see also Brändle & Brandl 2001). One likely reason for its high rank is the faster decay of *Carpinus betulus* wood compared with that of other broadleaf species. Saproxylic beetle species that occur in later decay stages might therefore colonize *Carpinus betulus*. This assumption is supported by *Carpinus betulus* logs having a mean decay niche position of saproxylic broadleaf specialists higher than that of almost all broadleaf trees tested

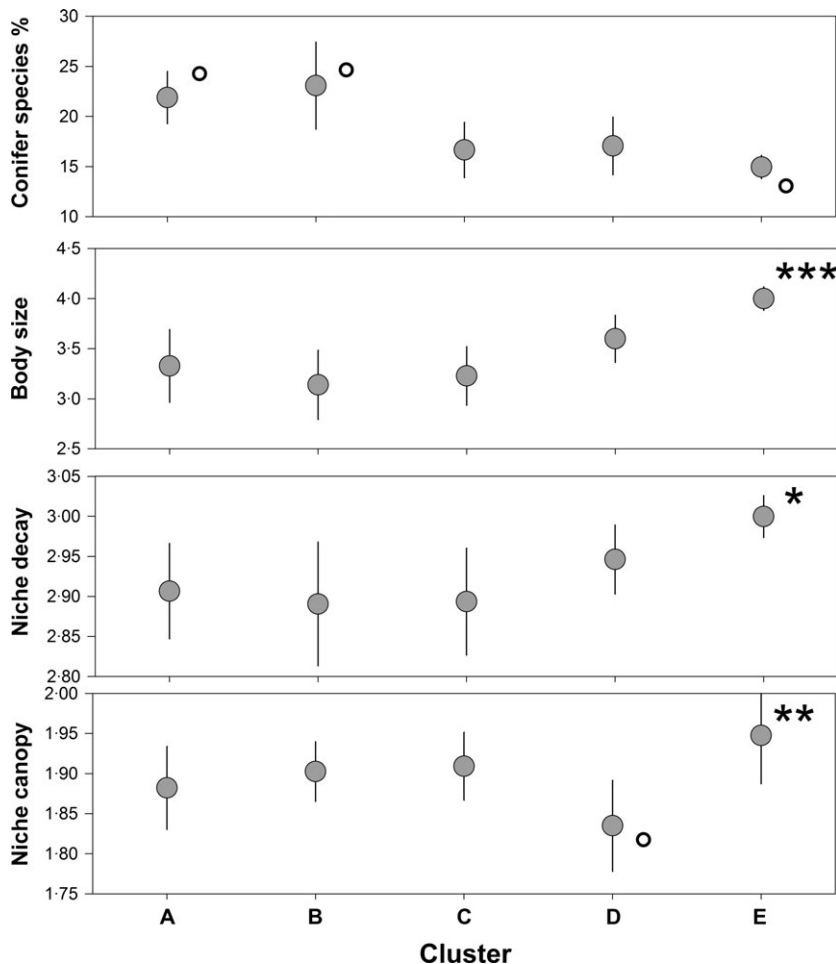


Fig. 5. Variation in the mean values of different traits (three ecological, one morphological) across the community sampled on one plot in 1 year. Clusters correspond to the five clusters created in Fig. 2 (A = conifer forests vs. beech forests; B = Schwäbische Alb vs. Hainich-Dün/Schorfheide-Chorin, C = Hainich-Dün, D = Schorfheide-Chorin, E = year 2011 vs. year 2010). Significant differences from the hierarchically remaining plots (see Fig. 2) were identified by a binomial generalized linear mixed model for each cluster indicated as ° $P < 0.1$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. These signs above the scatter indicate a positive influence on the cluster; those below indicate a negative influence. Note that the number of observations decreases from E to A to B to C and D (see Fig. 2).

(mean decay niche based on species: *Populus* sp. > *Carpinus betulus* > *Acer* sp. > *Tilia* sp. > *Prunus avium* > *Fraxinus excelsior* > *Fagus sylvatica* > *Betula pendula* > *Quercus* sp.). Preliminary data from the Biodiversity Exploratories Project on the decay process of our tested logs based on wood density loss suggested that *Carpinus betulus* wood decays second fastest, after *Betula pendula*, during the first years, and preliminary data on CO₂ emission suggest that *Carpinus betulus* logs have the highest decomposition activity among the studied tree species (Tiemo Kahl, unpublished data). Nevertheless, this does not completely explain the observed clear pattern, and further analyses are required.

Surprisingly, no specific higher rank values of *Quercus* sp. were detected in our experiment despite the exceptionally high species richness of associated specialist insect herbivore species (Brändle & Brandl 2001) and despite the highest preference of insects for hollow trees as hosts in a study of four broadleaf trees (Milberg *et al.* 2014). The intermediate ranking of oak might be explained by the position of the experimental logs on the ground and in shaded stands. Many oak specialists prefer sun-exposed dead wood (Zabransky 2004; Buse, Schröder & Assmann 2007; Franc & Gotmark 2008). In contrast, *Carpinus betulus* is a highly shade-tolerant tree species that regularly

grows in the shady middle strata of a forest stand, and thus, its dead wood is naturally often found in the shade.

Only in the first year was the host ranking significantly shaped by covariates. This may mirror the general trend of higher host specificity of saproxylic beetles foraging on the fresh cambium compared with those beetle species that occur during later decomposition stages. Chemical defence of trees decreases with progressing wood decomposition, and thus, early colonizers in particular need to overcome the chemical barriers (Wagner, Clancy & Lieutier 2002). It has also been shown that on broadleaf trees, many saproxylic beetles are linked to fungal colonization, which leads to higher species numbers in later stages of wood decay, whereas conifers harbour most species in the early fungal colonization stage (for spruce and poplar, see Saint-Germain, Drapeau & Buddle 2007).

We focused on three types of forest management in our study and found a clear difference between broadleaf and conifer stands, but no effect of forest protection, on host rankings. These results could be explained by mainly two factors. First, the major differences in phytophage and decomposer compositions between tree species are driven by the split between angiosperms and gymnosperms (Brändle & Brandl 2001). Secondly, even if half of the broadleaf stands studied were under protection with no

logging operations, the two categories cannot yet be distinguished by species composition and structures of typical managed stands (see Appendix S7, Supporting information) along a gradient of logging intensity of European beech forests (Gossner *et al.* 2013). In medium-aged beech stands (70–120 years) set aside without further management, trees have a low probability of death, and rich amounts of dead wood are lacking (Holzwarth *et al.* 2013).

The general findings discussed above are supported by the post hoc characterization of the clusters of our regression tree (Fig. 5). The proportion of conifer specialists was the most important trait explaining the separation in host ranking of planted conifer stands from beech stands, and furthermore the separation of the region Schwäbische Alb from the other regions. The separation in host ranking of the cluster of planted conifer stands from the cluster of beech stands seems to be obvious, but the separation of regions was unexpected as Schorfheide-Chorin is the region with the highest proportion of conifers and Hainich-Dün is the region with the lowest proportion. Thus, the high rankings of *Picea abies* combined with the high proportion of this tree species in the Schwäbische Alb might explain the separation of clusters. The composition of the second-year saproxylic beetle communities was dominated more by larger beetle species and by species of advanced decay stage and preferring shaded conditions (Cluster E in Fig. 4). This increase in large species in the second year might be explained by the longer life cycle of beetles of larger body size (Speight 1989). The increase in species in shaded conditions might be supported by the set-up of the logs in forest plots, with close canopy cover acting as an important habitat filter over time.

Overall, our dead-wood host experiment over 2 years revealed a clear ranking of hosts preferred by saproxylic beetles that deviates from host recordings prevailing in the literature and emphasizes variation in host ranking depending on forest management and region. Therefore, we suggest that dead-wood enrichment strategies consider the locally and regionally occurring tree species more comprehensively to increase saproxylic beetle diversity effectively. However, dead wood provides myriad features beyond host identity. Thus, we suggest further experiments that focus on dead-wood diameter, dead-wood moisture and microclimate and that include environmental contrasts other than management intensities. Large logs represent the type of dead-wood structure for which wood-inhabiting organisms and humans most intensively compete (Grove & Meggs 2003), and logs in Central European forests are usually exposed under canopy cover due to the prevailing non-clear-cutting logging strategies (Seibold *et al.* 2014b). Continuation of this experiment over years will reveal not only the importance of later decay stages of different tree species but also the importance of fungal colonization for saproxylic beetle assemblages.

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Data accessibility

-Species abundance data: uploaded as online supporting information.

-R scripts: uploaded as online supporting information.

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Supporting Information

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

Appendix S1. Beetle sampling and species list.

Appendix S2. Description of the statistical model.

Appendix S3. R-function.

Appendix S4. R-script.

Appendix S5. Data table beetles and host log matrix.

Appendix S6. Comparison of worth parameter with proportion of beetles ‘effectively specialized’.

Appendix S7. European wide comparison of study plots.