



## Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation



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### ABSTRACT

Vertical gradients of habitats are a typical characteristic of forest ecosystems. Sun-exposed dead wood in the upper canopy, for instance, provides a habitat for saproxylic beetles distinct from that in the more shaded dead wood below the canopy. Canopy research, however, is challenging due to both the limited accessibility and potential confounding effects of temperature on trapping probability when activity traps are used. We studied saproxylic beetle assemblages along a complete vertical gradient without bias caused by temperature effects on activity. Using crane-like constructions attached to the top of large Silver Fir trees (*Abies alba*), we exposed bundles of freshly cut branches of European Beech (*Fagus sylvatica*), Silver Fir and Norway Spruce (*Picea abies*) in three different vertical strata (upper canopy, mid-canopy and near the ground). The bundles in the upper canopy were fully exposed to the sun and the bundles in the mid-canopy and near the ground were in the shade. We allowed beetles to colonize the bundles of branches for one growing period and then reared beetles from each bundle over three years. The species composition of saproxylic beetle assemblages differed between bundles in the upper canopy and near the ground; bundles in the mid-canopy had an intermediate assemblage composition. The abundance of saproxylic beetles was higher near the ground than in the upper canopy, whereas the number of species showed the opposite pattern. Overlapping confidence intervals of sample-based rarefaction and extrapolation curves for species diversity indicate that estimated gamma diversity per stratum is similar across the three strata. Our results support earlier studies that revealed the importance of habitat heterogeneity as a driver of the biodiversity of taxa associated with dead wood. As we controlled for wood diameter and tree species diversity, our study suggests that the microclimatic variability within dead wood – and thus habitat heterogeneity for saproxylic beetles – is higher in the upper canopy than near the ground. For biodiversity conservation in forests, our results support a strategy of enhancing the number of trees with microhabitats, particularly those with dead branches in the upper tree crown. Dead branches and standing dead trees should only be removed, e.g. for safety reasons, if no other option is available.

### 1. Introduction

A distinct feature of forest ecosystems is the pronounced vertical axis that creates gradients of several abiotic and biotic factors (Nakamura et al., 2017). For example, the higher sun exposure and wind in the upper canopy leads to stronger evaporation than in the lower canopy (Parker, 1995; Shaw, 2004). Leaves and branches in the

upper canopy physiologically and structurally adapt to these abiotic conditions and differ from those in lower strata (Ulyshen, 2011, and references therein). Also fungi living on dead branches in the canopy have special strategies to cope with the strong tendency towards desiccation (Nunez, 1996). Many insect species have also adapted to life in the canopy (Basset et al., 2012, 2003), including a rich fauna of saproxylic, i.e. dead-wood-dependent, species (Schmidl and Bussler,

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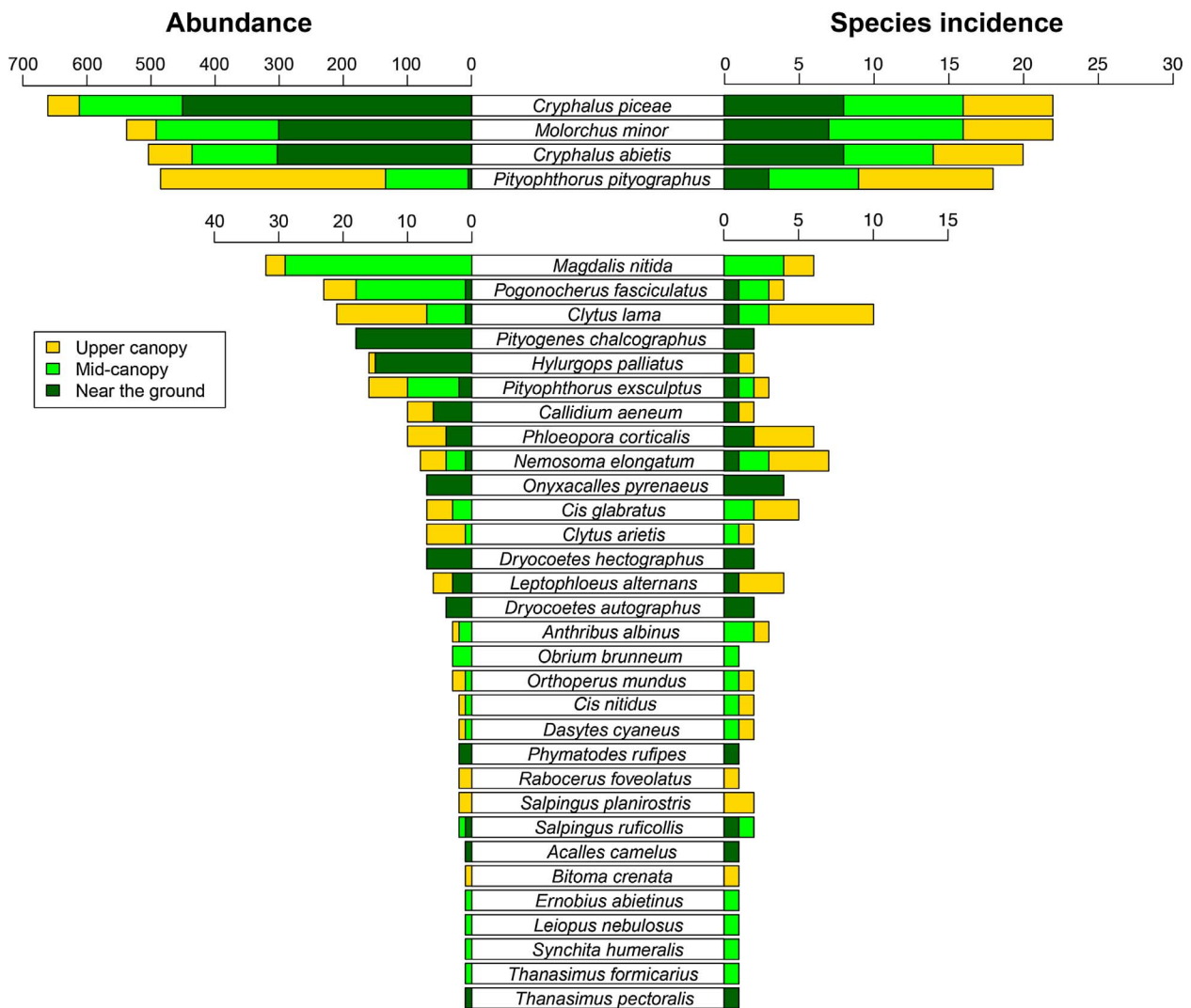


Fig. 1. Abundance and incidence of the 35 recorded saproxylic beetle species in bundles of dead branches placed in the upper canopy, mid-canopy and near the ground. For each bundle position, the incidence scale ranged from 0 to 10, with 10 indicating that the species was present in all 10 bundles at this position. Different strata are indicated by the bar colour. Note the different scale of the x-axes for the four most abundant species.

2008; Ulyshen, 2011).

For saproxylic insects, dead wood in the canopy provides a different type of habitat than dead wood on the forest floor, particularly when the forest floor is shaded; even within the canopy, different canopy layers can form a gradient of habitats (e.g. Weiss et al., 2016). Several factors that differ in the dead wood of different vertical strata could contribute to this gradient of habitats. First, many saproxylic insect species have a strong preference for particular microclimatic conditions, and thus, the species composition differs between sun-exposed and shaded dead wood (Seibold et al., 2016; Vodka et al., 2009). Second, many species differentiate between dead wood of different diameter classes, and the diameter distribution changes along the vertical axis, with dead wood of small diameter dominating the upper strata (Foit, 2010). Third, for insects associated with wood-decomposing fungi, differences in fungal species composition in different vertical strata (Unterseher et al., 2005; Unterseher and Tal, 2006) could influence assemblages of saproxylic beetles. Finally, colonization of new suitable substrate in the canopy might require airborne dispersal (Ulyshen 2011).

Most field studies comparing saproxylic beetle assemblages in different vertical strata have thus found differences in species composition (Foit, 2010; Maguire et al., 2014; Ulyshen and Hanula, 2007; Vodka et al., 2009; Weiss et al., 2016). Patterns of abundance, numbers of

species and species richness along the vertical axis, however, have been less consistent. Some studies found abundances and numbers of species to be higher in strata near the ground than in the canopy above (Müller and Goßner, 2010; Vodka et al., 2009; Weiss et al., 2016), whereas others found no significant difference (Maguire et al., 2014; Ulyshen and Hanula, 2007) or even the opposite pattern (Normann et al., 2016; Plewa et al., 2017; Ulyshen and Sheehan, 2017). Moreover, diversity patterns of saproxylic beetles along the vertical axis can differ between tree species (Bouget et al., 2011) and among different beetle guilds or taxa (Plewa et al., 2017; Ulyshen and Sheehan, 2017; Wermelinger et al., 2007), and might depend on the diversity metric analysed (Floren et al., 2014).

Canopy arthropod research faces two methodological challenges that might contribute to the inconsistency in the results. First, insect activity increases with increasing temperature (Liu et al., 1995). Thus, if activity traps, such as flight-interception traps, are used, as in most studies, higher abundances in the sunny upper canopy compared to those in the shady lower canopy could be a consequence of insect activity. An alternative to activity traps is the rearing of insects from bait logs or natural dead wood because this method is less confounded by effects of temperature on trapping probability (Bouget et al., 2011; Müller et al., 2015; Vodka et al., 2009). Two studies in which insects were reared on oak dead wood found higher abundances and/or

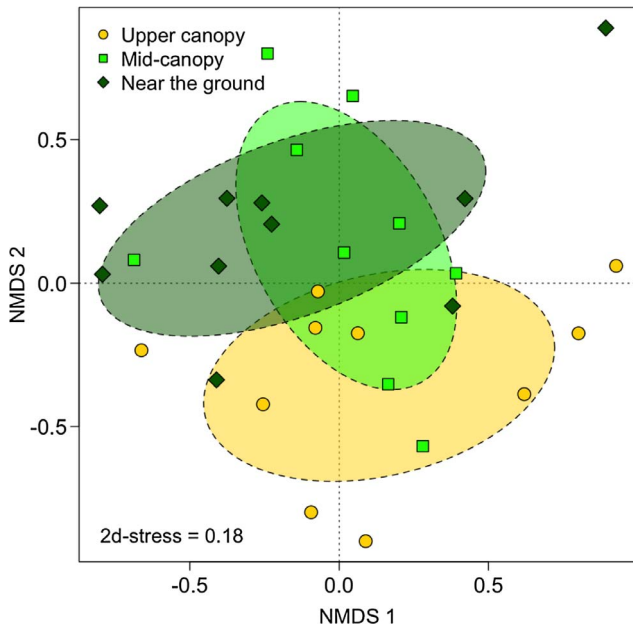


Fig. 2. Non-metric multidimensional scaling (NMDS) of the assemblage composition of saproxylic beetles reared for three years from 30 branch bundles from three different canopy strata (upper canopy, mid-canopy and near the ground). Ellipses represent the interquartile range of NMDS scores for each vertical stratum.

numbers of species of saproxylic beetles near the ground than in the canopy (Bouget et al., 2011; Vodka et al., 2009), but the opposite pattern of beetle abundance was found when beetles were reared on pine dead wood (Bouget et al., 2011). The second challenge of canopy research is reaching the uppermost canopy layer, which has the most extreme abiotic conditions; to facilitate sampling at the top of the forest, expensive equipment, such as cranes, is required (Nakamura et al., 2017). Studies excluding the uppermost canopy layer could miss an important part of the vertical gradient (Weiss et al., 2016).

Conservation of saproxylic biodiversity is strongly focused on dead wood on the forest floor and “habitat trees”, i.e. trees with particular microhabitats important for biodiversity (Kraus et al., 2016). Although abundant dead wood in the canopy is one criterion that defines a habitat tree, other aspects, particularly cavities, are usually the focus of scientists and practitioners because they host highly threatened and diverse fauna (Kraus et al., 2016; Larrieu et al., 2014; Müller et al., 2014). Despite an increasing awareness of the importance of trees with microhabitats, their power as a biodiversity surrogate is still under study (see Bouget et al., 2013). About 27% of the saproxylic beetle species in Europe are threatened (Nieto and Alexander, 2010), and

Table 1

Results from multiple comparisons of the differences in abundance and number of species of saproxylic beetles between the three vertical strata (upper canopy, mid-canopy and near the ground). Comparisons were based on quasi-Poisson linear mixed effect models. Values in bold indicate (marginal) significant results ( $p < .01$ ) and asterisks indicate significant results ( $p < .05$ ).

	Linear hypotheses	Estimate	Std. error	z-value	p-value
Abundance	mid-canopy–upper canopy	0.1794	0.2992	0.600	0.5486
	near the ground–upper canopy	<b>0.6705</b>	<b>0.2714</b>	<b>2.470</b>	<b>0.0135*</b>
	near the ground–mid-canopy	<b>0.4910</b>	<b>0.2563</b>	<b>1.916</b>	<b>0.0554</b>
Number of species	mid-canopy–upper canopy	-0.1542	0.1199	-1.286	0.1984
	near the ground–upper canopy	<b>-0.2513</b>	<b>0.1231</b>	<b>-2.041</b>	<b>0.0412*</b>
	near the ground–mid-canopy	-0.0972	0.1275	-0.762	0.4461

particularly those species that prefer sun-exposed dead wood have a higher Red List status than species that prefer dead wood in shady habitats (Seibold et al., 2015b). Thus, dead wood in the canopy might be particularly important for the conservation of saproxylic biodiversity. However, trees with high amounts of dead wood in the canopy are often felled or dead wood is removed by arborists for the safety of forest workers and the public.

The aim of this study was to investigate diversity patterns of saproxylic beetles in dead branches in tree canopies, less confounded by insect activity and along a vertical gradient that includes the highest stratum. We used crane-like arms attached to treetops to expose bundles of freshly cut branches for one growing season in the upper canopy exposed to the sun, in the mid-canopy in the shade and near the ground. We reared beetles from these bundles of dead wood over three years.

## 2. Methods

### 2.1. Study area and experimental design

Our study was conducted in the Bavarian Forest National Park, Germany (48°54'N, 13°90'E; approx. 650–900 m a.s.l.). We selected ten stands in mature montane mixed forests dominated by Norway Spruce (*Picea abies*), European Beech (*Fagus sylvatica*) and Silver Fir (*Abies alba*). In each stand, we selected the largest fir tree that ranged above the surrounding trees as a living pole. Arborists cut off the top of these trees at a diameter of 12 cm and a height of 26–47 m, depending on the

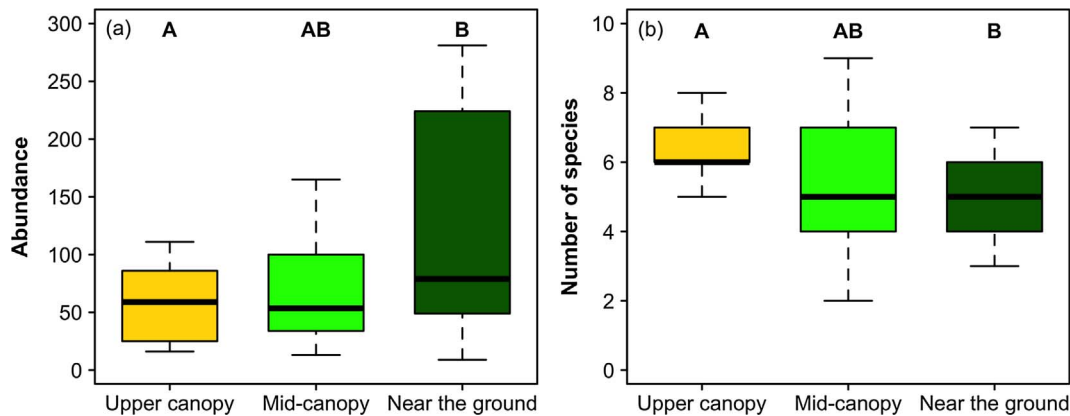


Fig. 3. (a) Abundance and (b) number of species of saproxylic beetles from three canopy strata (upper canopy, mid-canopy and near the ground). Significant differences between strata, based on quasi-Poisson linear mixed effects models, are indicated by upper-case letters.

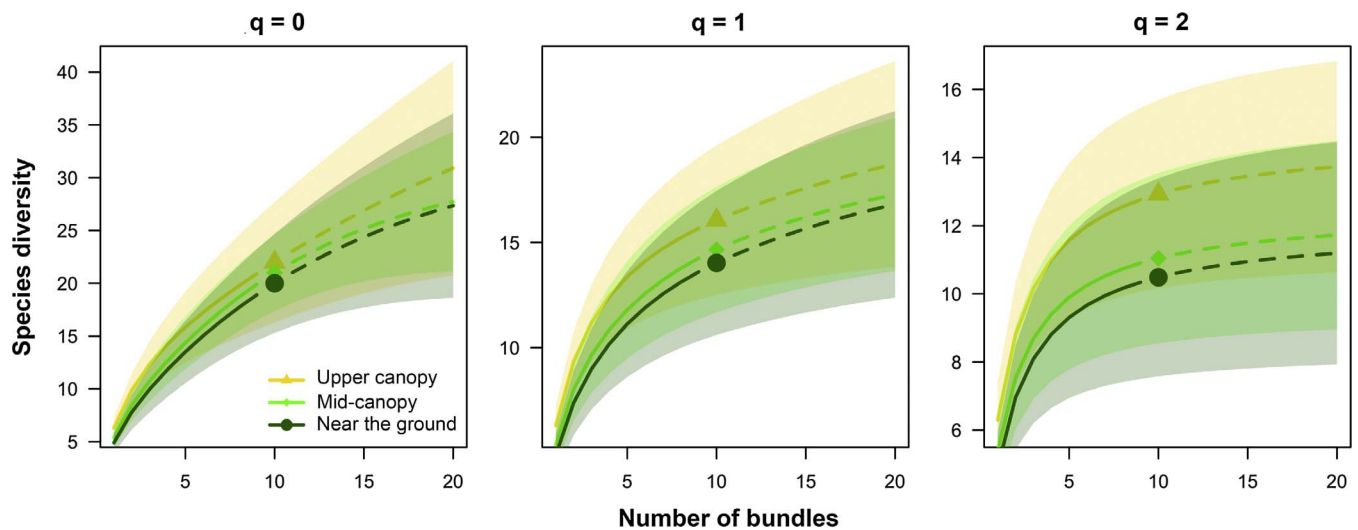


Fig. 4. Sample-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the actual sample size) of saproxylic beetle gamma diversity, along with 95% unconditional confidence intervals (transparent shading), of the beetles reared from bundles of dead branches placed in the three canopy strata (upper canopy, mid-canopy and near the ground). Species diversity was estimated for Hill numbers:  $q = 0$  (species richness),  $q = 1$  (exponential of Shannon's entropy index) and  $q = 2$  (inverse of Simpson's concentration index), as indicated. Solid symbols represent the total number of reference samples.

maximum height of the tree, and attached an aluminium arm with a line for pulling up loads at the top of the living pole (for details see Müller et al., 2013).

We placed three bundles of freshly cut branches in each tree and exposed them for a full growing period from late March to September 2013 to give saproxylic beetles the opportunity to colonize the dead wood. The first bundle was attached to the tree trunk 1 m above ground ("near the ground"), the second was placed in the mid-canopy in the shade ("mid-canopy") and the third was placed immediately below the aluminium arm, fully exposed to the sun ("upper canopy"). The actual above-ground height of the bundles in the mid- and upper canopy varied between stands depending on the height of the live crown base and the height of the trees (mid-canopy: 10–30 m; upper canopy: 25–46 m). To make the dead wood bundles, we cut living branches without signs of insect or fungal activity from the crown of spruce, fir and beech trees freshly felled near the study sites. Each bundle consisted of five thin branches (1–2 cm diameter) and three thicker branches (5–7 cm diameter) of each of the three tree species (24 branches per bundle) with a length of 50 cm. Bundles were wrapped tightly with a strong metal wire to ensure that no branches were lost.

## 2.2. Sampling of saproxylic beetles

We retrieved all bundles from the trees in September 2013 and placed each bundle in a non-transparent PVC barrel (50 cm diameter and 90 cm length) for three years until October 2016. Barrels were placed under a roof at ambient temperature to provide shade and avoid overheating; barrels had an opening covered by a fine mesh to allow air circulation. A transparent collecting jar filled with ethanol was mounted to each barrel to collect and preserve emerging beetles attracted to the light. Collecting jars were emptied regularly, and all beetles found inside the barrels were collected and added to the sample. All beetles were sorted and identified at the species level by B. Büche (Berlin, Germany).

To evaluate whether beetle assemblages differ in their preference for canopy openness or dispersal ability, we obtained the mean niche position for canopy openness (ranging from 1 = open forests to 3 = closed forests) and mean body size of each species as a proxy for dispersal ability (den Boer, 1990) from Seibold et al. (2015b). Further proxies for dispersal ability included wing loading (body mass divided by wing area) and the wing aspect ratio (wing length divided by wing width; Gibb et al., 2006) which we calculated from measured values of

wing area, wing length, wing width and biomass of one fully developed individual of each species (for details, see Fig. S1 in Supplementary Material).

## 2.3. Statistical analyses

All analyses were performed in R (R Core Team, 2017). We used non-metric multidimensional scaling (NMDS) and distance-based analysis of similarity (ANOSIM) to visualize and test differences within the species community composition among the three different vertical strata (Clarke, 1993). ANOSIM was calculated for both presence-absence and abundance data. The obtained p-values were adjusted according to Benjamini and Hochberg (1995). NMDS based on Bray-Curtis dissimilarity distances of presence-absence data were calculated using the *metaMDS* function in the add-on package *vegan* (Oksanen et al., 2016). To test for effects of vertical strata on the alpha diversity of saproxylic beetles (abundance and number of species), we applied quasi-Poisson generalized linear mixed models with penalized quasi-likelihood. We treated stand as a random term in all models to control for effects of different stand characteristics. Calculations were performed with the *glmmPQ* function in the add-on package *MASS* (Ripley, 2015). The three vertical strata (upper canopy, mid-canopy and near the ground) were simultaneously compared and p-values were adjusted for multiple testing using the function *glht* in the add-on package *multcomp* (Hothorn et al., 2008). No indications for spatial autocorrelation between sites were found when we visually evaluated spline correlograms calculated using the *spline.correlog* function of the add-on package *ncf* (Bjornstad and Falck, 2001) for the residuals of the models (Fig. S2). To estimate gamma diversity for each of the three vertical strata, we used a sample-based rarefaction-extrapolation approach, which estimated the rate of increase in the number of species with increasing number of samples and extrapolated the number of species per stratum to twice our actual sample size. Calculations were performed with the *iNEXT* package (Chao et al., 2014) for the three components of species diversity represented by the Hill series ( $q = 0$ , species richness;  $q = 1$ , exponential of Shannon's entropy index;  $q = 2$ , inverse of Simpson's concentration index). Significant differences in estimated gamma diversity between canopy strata were judged by non-overlapping confidence intervals (Schenker and Gentleman, 2001).

### 3. Results

The three years of rearing from the 30 samples yielded 2408 individuals of saproxylic beetles belonging to 35 species (Fig. 1, Table S1). The number of individuals (number of species) that emerged during the first, second and third year was 662 (15), 1399 (25) and 347 (9), respectively. Some species, such as *Cryphalus abietis* and *Cryphalus piceae*, were recorded only in the first and second year; species with a typical larval development time of more than one year, such as *Clytus lama* and *Clytus arietis*, were only recorded in the third year (Table S1). Twenty species were recorded only in the second and/or third rearing year (Table S1). Four highly abundant species (*Cryphalus piceae*, 661; *Molorchus minor*, 538; *Cryphalus abietis*, 504; and *Pityophthorus pityographus*, 485) accounted for 91% of all individuals, and 16 species sampled were represented by 3 or fewer individuals (Fig. 1).

The composition of saproxylic beetle assemblages differed between the upper canopy and near the ground (Fig. 2; Adonis:  $p_{(\text{presence-absence})} = 0.03$ ,  $p_{(\text{abundance})} = 0.03$ ). The mid-canopy had an intermediate assemblage composition of saproxylic beetles (Fig. 2), which did not differ significantly from that of the upper canopy ( $p_{(\text{presence-absence})} = 0.36$ ,  $p_{(\text{abundance})} = 0.51$ ) and near the ground ( $p_{(\text{presence-absence})} = 0.30$ ,  $p_{(\text{abundance})} = 0.21$ ). None of the community-weighted mean traits related to canopy openness and dispersal ability (i.e. body size, wing loading and wing aspect ratio) differed significantly between strata (Fig. S1).

The abundance of saproxylic beetles near the ground was significantly higher than in the upper canopy and marginally significantly higher than in the mid-canopy (Fig. 3; Table 1). The numbers of species showed the opposite pattern, with significantly more species in the upper canopy than near the ground (Fig. 3; Table 1). The number of species in the mid-canopy did not differ significantly from that of the other two strata. Confidence intervals of the sample-based rarefaction and extrapolation curves overlapped indicating that the estimated gamma diversity of saproxylic beetles was similar across canopy strata for all three Hill numbers (Fig. 4).

### 4. Discussion

Overall, we found that saproxylic beetle assemblages in dead branches placed in different canopy strata differ in composition and alpha diversity, both of which changed gradually with increasing vertical position. The abundances of saproxylic beetles were highest near the ground, but the number of species was highest in the upper canopy. Gamma diversity, however, did not differ between strata.

The rearing of insects from bait logs (or in our case, dead branches) can be an alternative to flight-interception traps for overcoming the effects of temperature on insect activity and sampling probability (e.g., Bouget et al., 2011; Müller et al., 2015; Vodka et al., 2009). Our results indicated that rearing is less biased by the activity of adult insects than activity traps as we found higher abundances near the ground than in the upper canopy (Fig. 2), even though temperature is lower in the shady understory. However, fewer insect individuals are usually sampled by rearing than by flight-interception traps which can hamper statistical analyses (Birkmoe and Sverdrup-Thygeson, 2015; Plewa et al., 2017). Moreover, further research is necessary to assess how rearing conditions affect mortality rates of larvae, in particular if bait logs have been colonized under heterogeneous environmental conditions but reared under homogenous conditions. The use of bait dead wood allow standardization of the type of dead wood, such as fresh branches, which might be necessary to be able to identify mechanisms behind observed biodiversity patterns (Seibold et al., 2015a). However, this means that only species associated with this type of dead wood can be recorded and not the overall biodiversity. As 60% of the individuals recorded within the three years of our study emerged during the second year, including several species that did not emerge during the first year (Table S1), rearing should be conducted for at least two years. Our

results also indicate that canopy arthropod studies need to cover the full vertical gradient, including the uppermost canopy, because most differences were only observed between the near-ground and upper canopy strata but not between the near-ground and mid-canopy strata (Figs. 1 and 2).

In line with most studies on saproxylic beetles in the canopy (Foit, 2010; Maguire et al., 2014; Plewa et al., 2017; Ulyshen and Hanula, 2007; Vodka et al., 2009; Weiss et al., 2016), we found a clear difference in species composition between the branches placed near the ground and in the upper canopy. The species composition in the branches in the mid-canopy overlapped with those of the other two strata (Fig. 2), which suggests a gradual turnover of species along the vertical axis. As we standardized the substrate by using freshly cut branches of set diameters, this turnover in species composition cannot be driven by differences in the diameter of the dead wood. We did not find any indication that changes in species composition are driven by preferences for sun exposure or dispersal ability, as none of the community-weighted mean traits differed between strata (Fig. S1). However, the mean niche position for canopy openness actually refers to the preference of a species for sunny or shady forests (Möller, 2009) and might not represent the preference for particular microclimates along the vertical axis. To further disentangle the role of vertical position and sun exposure, further experiments are required that compare beetle assemblages along vertical and horizontal gradients of sun exposure.

The observed patterns of higher abundances near the ground than in the upper canopy are in line with earlier rearing data from beech–fir forests (Bouget et al., 2011). The high abundances near the ground in our study were largely because of the three most dominant beetle species, which occurred mostly near the ground (Fig. 1). Higher abundances near the ground than in the canopy could be caused by the higher amounts of dead wood on the forest floor than in the canopy, as more colonizers of dead wood would be found near the ground. However, if the higher abundance near the ground was caused by more colonizing individuals, then – according to the more-individuals hypothesis (Wright, 1983) – this should also lead to higher numbers of species near the ground as observed in other studies (Bouget et al., 2011; Vodka et al., 2009; Weiss et al., 2016). We, however, found higher numbers of species per bundle in the upper canopy than near the ground (Fig. 3). A possible explanation for this pattern is that more species with a preference for small-diameter dead wood occur in the canopy than near the ground (Ulyshen, 2011), and thus, a larger species pool of potential colonizers is present in the canopy. Another possible explanation is that habitat heterogeneity, i.e. a higher number of niches per volume dead wood, is higher in the upper canopy than near the ground because microclimatic differences within dead wood are more pronounced in the upper canopy due to direct sun exposure. High sun exposure creates a strong contrast between dry and warm branch parts facing the sun and the cool and moist branch underparts that host different saproxylic beetle assemblages (Graham, 1924). Similarly, higher habitat heterogeneity due to microclimatic variability was used to explain why species richness but not abundance of saproxylic beetles increased with increasing amount of dead wood in sunny forest gaps, whereas neither richness nor abundance was affected by the amount of dead wood under a closed canopy (Seibold et al., 2016). Although alpha diversity, i.e. the number of saproxylic beetle species per bundle, was higher in the upper canopy than near the ground, gamma diversity, i.e. the rarified-extrapolated species diversity per stratum, was similar for all three strata. This difference in alpha and gamma diversity patterns might be explained by higher habitat heterogeneity between sites at the ground level than in the canopy.

Our study showed that dead wood of small diameter in the upper canopy and near the ground host overall similar numbers of saproxylic beetle species (i.e. estimated gamma diversity; Fig. 4), but the assemblages in the two strata comprised different species (Fig. 2). This suggests that dead wood of small diameter in both strata is of considerable importance to conserve saproxylic beetle biodiversity. Activities that

reduce amounts of these types of dead wood, such as cutting dead branches or dead trees for safety reasons or harvesting logging residuals as fuel wood, could threaten the biodiversity of saproxylic beetles. Especially dead wood in the upper canopy, which develops only slowly as a result of tree senescence, should be retained as much as possible, e.g. by retaining trees with a high number of dead branches in the canopy as habitat trees. The cutting of dead branches or felling of dead trees should be the very last option when it comes to safety issues (see Stokland et al., 2012 p. 399 for a decision tree). Other options, such as restricting access to the tree or informing visitors, could be considered first, if any action is required at all. The creation of snags and downed dead wood as conservation measures to promote biodiversity have been evaluated and proved to be successful (Seibold et al., 2015a), but further experiments are required to test how dead wood in the canopy can be created to promote biodiversity in this stratum. Moreover, further investigations under standardized conditions are needed that test whether dead wood of small diameter near the ground can substitute for dead wood in the canopy if certain microclimatic conditions are met.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.11.052>.

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