



Saproxylic beetles trace deadwood and differentiate between deadwood niches before their arrival on potential hosts

MARLENE GRAF,^{1,2} LUDWIG LETTENMAIER,³ JÖRG MÜLLER^{2,4} and JONAS HAGGE^{5,6}

¹Faculty of Environment and Natural Resources, Albert-Ludwigs-University Freiburg, Freiburg, Germany, Grafenau, Germany, ²Bavarian Forest National Park, Grafenau, Germany, ³Department of Biology, Faculty of Science, University of Hradec Králové, Hradec Králové, Czech Republic, ⁴Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Rauhenebrach, Germany, ⁵Forest Nature Conservation, Georg-August-University Göttingen, Göttingen, Germany and ⁶Forest Nature Conservation, Northwest German Forest Research Institute, Hann, Münden, Germany

Abstract. 1. Deadwood provides a variety of habitats for saproxylic beetles. Whereas the understanding of the drivers promoting saproxylic beetle diversity has improved, the process of deadwood colonisation and beetle's potential to trace resources is poorly understood. However, the mechanisms facilitating deadwood detection by saproxylic beetles appears to be essential for survival, as deadwood is usually scattered in time and space.

2. To investigate whether saproxylic beetles distinguish before their arrival on potential hosts between alive trees and deadwood (lying, stumps, standing), deadwood arrangement (aggregated, distributed) and different heights on standing resources (bottom = 0.5 m, middle = 4–5 m, top = 7.30–11.60 m), we sampled saproxylic beetles with sticky traps in a deadwood experiment.

3. We found on average 67% higher abundance, 100% higher species numbers and 50–130% higher species diversity of colonising saproxylic beetles consistently for all deadwood types compared to alive trees with a distinct community composition on lying deadwood compared to the other resource types. Aggregated deadwood arrangement, which is associated with higher sun-exposure, had a positive effect on species richness. The abundance, species number and diversity, was significantly higher for standing deadwood and alive trees at the bottom section of tree trunks. In contrast to living trees, however, the vertical position had an additional effect on the community composition on standing deadwood.

4. Our results indicate that saproxylic beetles are attracted to potential deadwood habitats and actively select specific trunk sections before arriving on potential hosts. Furthermore, this study highlights the importance of sun-exposed resources for species richness in saproxylic beetles.

Key words. Deadwood, experiment, host discrimination, host selection, microclimate, saproxylic beetles, vertical stratification.

Introduction

Deadwood plays an important role for forest biodiversity by providing a huge variety of habitats for saproxylic species. Saproxylic species obligatorily depend on deadwood during at least one stage of their life cycle (Speight, 1989). Within the

Correspondence: Marlene Graf, Faculty of Environment and Natural Resources, Albert-Ludwigs-University of Freiburg, Freiburg, Germany. E-mail: marlene.graf@yahoo.de

community of saproxylic insects, the order Coleoptera represents a major and highly diverse taxa (Grove, 2002). Saproxylic beetle species show different preferences in host selection, which include tree species identity and decay stage (Stokland, 2012; Müller *et al.*, 2020), wood diameter (Siitonen & Stokland, 2012) and microclimate (Jonsson & Stokland, 2012; Seibold *et al.*, 2016; Müller *et al.*, 2020). In addition, it is known that saproxylic beetle species specialise in standing, lying or stump deadwood (Hjältén *et al.*, 2010). Whereas associations between deadwood types and species numbers as well as species compositions could be observed with respect to the place for their larval development (Jonsell & Weslien, 2003; Gibb *et al.*, 2006; Hedgren, 2007; Hjältén *et al.*, 2010; Bouget *et al.*, 2012), it is not yet known whether this biodiversity pattern is also reflected in the habitat selection process, that is, whether saproxylic beetles are able to distinguish their preferred host while flying and specifically land on it. The mechanism determining the recognition of deadwood resources is not yet fully understood. For instance, two hypotheses are being used as possible explanation for the host selection of bark beetle species. For some species, resource discrimination seems to occur after landing by assessing their suitability due to short-range olfactory and gustatory cues, named as the *random landing hypothesis* (Hynum & Berryman, 1980; Moeck *et al.*, 1981). Other species are supposed to be guided to their preferred habitat by associated emissions of volatile organic compounds (VOC), named as the *primary attraction hypothesis* (Anderson, 1977; Tunset *et al.*, 1993; Brattli *et al.*, 1998). However, the two hypotheses are not mutually exclusive. The emission of VOC by deadwood resources facilitates the detection on stand scale but not the precise localisation of the source. Potential hosts are assessed after landing, hence, mistaken landings on neighbouring non-hosts occur (Saint-Germain *et al.*, 2007). Long- and short-distance orientation might also rely on the processing of cues originating from different sources, such as decaying wood or pre-colonised fungi; a strategy which seems to be used by saproxylic species of Heteroptera (Seibold *et al.*, 2014; Koban *et al.*, 2016). The specialisation of saproxylic beetles on specific habitats for food intake or reproduction requires continuous resource availability and the ability of the species to track deadwood. Narrow habitat requirement ranges of saproxylic beetles suggest that there are various abiotic and biotic factors and chemical processes during the decay that induce the emission of different VOC bouquets bearing the respective information (Holighaus & Schütz, 2006; Leather *et al.*, 2014).

It is well established that the degree of canopy cover influences the degree of solar radiation and thus modulates microclimatic conditions within the forest stand (Kermavnar *et al.*, 2020; Müller *et al.*, 2020; Thom *et al.*, 2020) and deadwood objects (Forrester *et al.*, 2012), which might influence the colonisation process of saproxylic beetles. For instance, canopy openness leads to increased air temperatures, which can implicate higher soil temperature, whereas the concomitant higher rainfall and a decreased transpiration can increase soil moisture (Muscolo *et al.*, 2014). Sunlight reaching the ground in large canopy gaps is significantly higher than in scattered small canopy gaps, considerably influencing temperature and vapour pressure deficit (Thom *et al.*, 2020). In contrast, forest floors under closed

canopy exhibit lower mean temperatures and are buffered against high temperature fluctuations (De Frenne *et al.*, 2019).

Natural disturbances of larger scale and the associated death of trees create not only canopy gaps but also larger amounts of aggregated deadwood (Müller *et al.*, 2010). Grouped deadwood might facilitate olfactory as well as visual identification of hosts by saproxylic beetles (Sverdrup-Thygeson & Ims, 2002; Saint-Germain *et al.*, 2007). Since in some species the integration of visual and olfactory cues mediate the host selection process (Strom *et al.*, 1999; Campbell & Borden, 2006, 2009; Mayfield & Brownie, 2013), it is likely that deadwood will be easier to detect for beetles in open areas than it would be among many non-hosts in dense forests (Sverdrup-Thygeson & Ims, 2002). Consequently, canopy openness and the spatially dense accumulation of deadwood originating from natural events might positively mediate the host colonisation process and thus, promote species diversity.

Temperate forest stands can be generally stratified into different horizontal layers, which bear not only different microclimatic conditions but also different microhabitats and species interactions (Bouget *et al.*, 2011). Many arthropod taxa become less abundant, species rich or diverse with increasing height above the forest floor (Müller & Goßner, 2010; Ulyshen, 2011). Standing deadwood represents a heterogeneous resource, exhibiting almost twice as many microhabitats per tree than alive trees (Vuidot *et al.*, 2011), possibly because standing deadwood decomposes variably due to vertical microclimatic variations. A study by Levy (1982), which examined the fungal colonisation of fence posts, showed that the standing deadwood (albeit without root connection) can be divided in sections differing in terms of moisture content and fungal communities.

In order to explore whether the diversity patterns found for saproxylic beetles colonising deadwood is also reflected during host-seeking process, we used sticky traps on different deadwood types and alive trees in an experiment with plots of different deadwood arrangement and with traps in three different heights. We tested the following three hypotheses. (i) We expect that saproxylic beetles can distinguish between alive trees and different deadwood types before their arrival (i.e., while flying or before accessing the potential host by crawling from the ground), resulting in higher abundances, higher species numbers, increased diversity and a distinct community composition of colonising saproxylic beetles on deadwood compared to alive trees (primary attraction hypothesis). (ii) The higher degree of canopy openness, that is, higher sun-exposure, and the spatially dense accumulation of deadwood on plots with an aggregated deadwood arrangement positively mediates the microclimatic conditions. Hence, we anticipate higher abundance, increased species numbers and diversity and a different species composition of saproxylic beetles on plots with open canopy and aggregated deadwood than on those with closed canopy and distributed deadwood. (iii) We assume that saproxylic beetles are able to detect the vertically different microclimatic conditions on standing deadwood. Therefore, we expect a vertical distribution pattern of abundance, species number and diversity and a change of species composition between different height levels on standing deadwood and alive trees. We anticipate that the pattern will be more pronounced on standing deadwood than on alive trees.

Materials and methods

Study site and experimental design

Our study is part of a deadwood experiment encompassing a set of plots with five replications (hereinafter referred to as blocks) originating from the BioHolz project (www.bioholz-projekt.de) (for details, see Thom *et al.*, 2020). Four blocks are located in the Bavarian Forest National Park and one in a nearby forest in Thurmansbang, in south-east Germany. In 2015, plots had been established which all are dominated by European beech (*Fagus sylvatica* L.). Each plot covers an area of 50 m × 50 m (i.e., 2500 m²) of which ~25% of basal area had been manipulated in order to create deadwood in two different arrangements entailing different canopy covers. The manipulation had either been applied to a group of trees in the plot centre (25 m × 25 m, 625 m²), resulting in aggregated deadwood accumulations, or to individual trees spread randomly across the plot, resulting in a distributed deadwood arrangement. Consequently, the plots exhibited one large or several small canopy gaps, that is, a more open or closed canopy (Fig. Fig. 1). A study carried out on the same study plots showed that on the plots with distributed arrangement of deadwood sunlight reaching the ground is limited to 3–10%, whereas on plots with aggregated arrangement of deadwood on average ~15% of sunlight reach the ground (Thom *et*

al., 2020). In addition, forest floors under closed canopy do not only exhibit lower mean temperatures but are also buffered against high temperature fluctuations (De Frenne *et al.*, 2019). Hence, canopy openness, which modulates microclimatic conditions on stand and resource-level, is therefore often used as surrogate for microclimatic conditions on the plots (Seibold *et al.*, 2016). On the other hand, this manipulation entails different spatial distributions of deadwood (aggregated vs. distributed), which might result in differences in VOC concentration and composition on the plot, possibly influencing the colonisation process. Both factors are represented by the variable *aggregated and distributed arrangement* and hereinafter referred to as such.

Within the remaining gaps on the plots, three different deadwood types from beech (lying, standing and stump deadwood) had been created in four different combinations which were replicated in aggregated and distributed deadwood arrangement, respectively (Thom *et al.*, 2020). Standing deadwood was created by cutting the treetop below the first strong branch of the crown. To create lying deadwood, beeches were felled and their remaining stumps were considered as additional independent deadwood type. For this study, 10 plots of the experiment were chosen, which comprise all three deadwood types (Fig. Fig. 1). On each plot, eight sampling positions representing different resource types and different vertical positions were selected (Fig. Fig. 1).

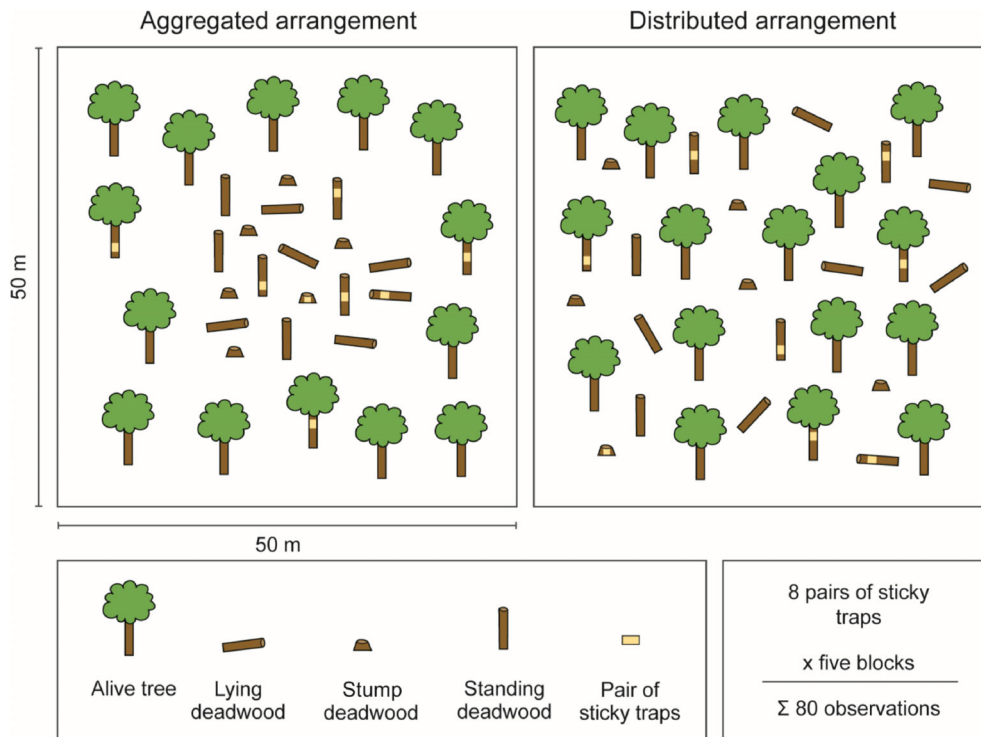


Fig 1. Sampling design. Colonising saproxylic beetles were sampled in a deadwood experiment using sticky traps. Half of the 10 experimental plots were treated with an aggregated deadwood arrangement (left panel) and half with a distributed arrangement (right panel). The 10 plots were arranged in a block design with one aggregated and one distributed plot per block. On each plot eight sampling positions representing different resource types and different vertical positions were selected.

Data collection

In order to investigate the process of deadwood colonisation, we recorded the arrival of saproxylic beetles on different resource types by using sticky traps. The traps consisted of a plastic sheet of 14.8 × 10.5 cm (ISO 216: A6), which was attached to selected objects and subsequently, glue-brushed (transparent insect glue, F. Schacht GmbH & Co. KG, Germany). Albeit smaller sample sizes compared to other sampling methods, sticky traps are useful for studying the approach and colonisation of deadwood by saproxylics because this sampling technique captures insects as they land on the traps (Collins *et al.*, 2002; Saint-Germain *et al.*, 2006, 2007; Eichholz *et al.*, 2019). This clearly distinguishes them from other passive methods such as flight intercept and stem emergence traps, which produce larger sample sizes but also catch significant numbers of non-saproxylic individuals passing through the forest stand or saproxylic species that already had detected and colonised the substrate, respectively (Alinvi *et al.*, 2007). Moreover, the abandonment of baiting techniques allowed testing for the random landing hypothesis and primary attraction hypothesis without distorting the results. However, in addition to specimens that have landed on the deadwood, sticky traps probably catch species and individuals that arrive on deadwood by crawling from the forest floor onto potential hosts or that have developed and emerged from the substrate beforehand.

We sampled during the years 2017 and 2018, which represent the second and third year after the deadwood creation in the experiment. In total, 160 sticky traps per year were used and left in place for 1 week at the beginning of June, which is the time of the highest activity of saproxylic beetles for the study region. The daily mean temperature recorded by a nearby climate station (Zwiesel) was 16.5 °C and 17.5 °C during the sampling period in 2017 and 2018, respectively (long-term mean of 1998–2018 for this time period 15.2 °C, Deutscher Wetterdienst, DWD). We sampled on standing deadwood (beech whose treetops had been removed), lying deadwood (obtained by felling beeches with removed tree-tops), stump deadwood (remaining from the downed trees) and surrounding alive beeches, respectively (Fig. 1). In order to test for vertical distribution of saproxylic beetles, we attached sticky traps at different heights on standing deadwood and alive trees. Therefore, sticky traps were attached on standing deadwood choosing the stem section near the ground at 50 cm height (*bottom section*), at 4 m height representing the middle of the trunk (*middle section*) and 50 cm below the cutting edge with height ranging between 7.30 and 11.60 m across the plots (*top section*). To ensure consistency within plots, the height of the trap at the top section installed on deadwood (50 cm from the cutting edge) was transferred to the alive tree, accordingly. To avoid pseudo-replication, one trunk/tree per height was chosen (Fig. 1). The variable representing the height of the trap is hereinafter referred to as *vertical position*. Per study object and vertical position, we attached a sticky trap each to the north- and south-facing side of the trunk. On lying deadwood, the sticky traps were placed on the upper side at a distance of 50 and 100 cm from the cutting edge. In analyses, each of these pairs of sticky traps were considered as one sample. All captured beetles were counted, freed from glue with washing solvent and preserved in 70% ethanol. For our analyses, we included only beetles

classified as strictly saproxylic according to the reference list for Germany (van Schmidl & Bußler, 2004).

Statistics

All statistical analyses were conducted in R 3.5.2 (www.r-project.org). To increase sample size and yield sufficient numbers for abundance and number of species, datasets of 2017 and 2018 were merged. Pairs of sticky traps were pooled according to resource and vertical position, resulting in a dataset of 80 species assemblages (i.e., species by trap matrix). In order to investigate mechanisms influencing the colonisation process, we built four mixed effects models using the ‘glmer’ function in the add-on package ‘lme4’ (Bates *et al.*, 2015) with either abundance or number of species of saproxylic beetles as response variable. First, a model each was built to test the relationship to the variables resource type (i) and deadwood arrangement (ii). Second, we modelled abundance or species richness as a function of the vertical position of the traps differentiating between alive tree and standing deadwood (iii). To account for site and tree individual related variation due to the experimental design, study site and tree ID were added as random terms to the model (Baayen, 2012). Based on the experimental design, we built separate models implementing respective subsets of the data with Poisson distribution. The model that tested the effect of resource type and deadwood arrangement was based on data obtained from stump and lying deadwood and traps attached to the bottom section of standing deadwood and alive tree. In contrast, for an impact of vertical position, only data from alive trees and standing deadwood were included. Post hoc Tukey’s tests were used to determine pair-wise comparisons among resource types and vertical positions using the ‘glht’ function which is included in the R package ‘multcomp’ (Hothorn *et al.*, 2008).

For species diversity analysis, a sample-based rarefaction/extrapolation based on the framework of Chao *et al.* (2014), which is implemented in the R package ‘iNEXT’ (Hsieh *et al.*, 2019), was used. Species accumulation curves of three diversity indices, species richness, Shannon diversity and Simpson diversity, were computed for the different resource types, vertical positions and deadwood arrangements using sampling-unit-based incidence data. Species richness ($q = 0$) weights all species equally regardless of their relative abundance, that is, rare count as much as common species. Shannon’s entropy index ($q = 1$) and the inverse of Simpson’s concentration index ($q = 2$) can be interpreted as the effective number of common and dominant species, respectively. Accumulation curves of different orders of q were created for the different resource types, vertical positions and deadwood arrangements. Non-overlapping confidence intervals are considered as significant different at a level of 5% among the estimated species richnesses (Chao & Jost, 2012).

The effect of resource type, deadwood arrangement and vertical position on the community composition of colonising saproxylic beetles was tested by non-parametric multivariate analysis of variance using distance matrices with the ‘adonis’ function implemented in the ‘vegan’ package with 1000

permutations (Anderson, 2001). In order to analyse the community composition on resource types and deadwood arrangements, subsets of the data were used that only comprise sticky traps that had been attached at the bottom section of standing deadwood and alive tree, on stump and lying deadwood. The analysis of changes in community compositions along the vertical positions of traps was performed separately for standing deadwood and alive trees and included data that were grouped accordingly. Each analysis was conducted for the entire group (resource type, vertical position and deadwood arrangement) and community changes among subsets of the groups were tested by pairwise comparisons, namely between the four resource types and three vertical positions, based on the Bray–Curtis dissimilarity distances. Regarding the experimental design, *block* was included as a grouping factor, constraining the permutations within the group. The obtained *P*-values were adjusted in order to control the false discovery rate for multiple testing following the method of Benjamini and Hochberg (1995).

The indicator species analysis (IndVal) (Dufrene & Legendre, 1997) was computed as a further means in order to examine the specificity of families among deadwood arrangements, resource types and vertical positions on standing resources. This method provides an indicator value (IndVal) for each family as percentage based on measures of specificity (abundance) and fidelity (frequency of occurrence) (Dufrene & Legendre, 1997). These values were computed, using the ‘labdsv’ package (Roberts, 2019). Indicator species values were computed using the subsets of the data analogously to prior described statistical analysis. The obtained *P*-values were adjusted applying the method of Benjamini and Hochberg (1995).

Results

In total, 122 species of strictly saproxylic beetles (1223 individuals) were sampled (for the species list, see Table S1). Merging the total number of traps across orientations (north and south) and sampling periods, resulted in 80 samples that exhibited on average 6 ± 5 species of saproxylic beetles (15 ± 26 individuals; mean \pm SE).

Colonisation of deadwood by saproxylic beetles

The mixed-effect models revealed that the abundance of colonising saproxylic beetles was on average $\sim 67\%$ and the species number $\sim 100\%$ higher on deadwood compared to alive trees (Fig. 2; Table S2). Also, species diversity of colonising saproxylic beetles on deadwood were consistently higher on deadwood than on alive trees for all three values of q {0,1,2}, that is, for species richness, Shannon diversity and Simpson diversity, respectively (Fig. 4 and S1; Table S4). The confidence intervals of the species accumulation curve of deadwood and alive trees converge and overlap with increasing order of q , respectively (Fig. S1). Thus, predominantly rare species were driving higher species diversity on deadwood resources compared to alive trees. Among the three different deadwood types of standing, lying and stump deadwood, we found no differences in abundance, species number and species diversity of colonising saproxylic beetles (Fig. 2 and Fig. 4; Tables S2 and S4). Multivariate analysis of variance showed significant differences in terms of community composition between lying deadwood and

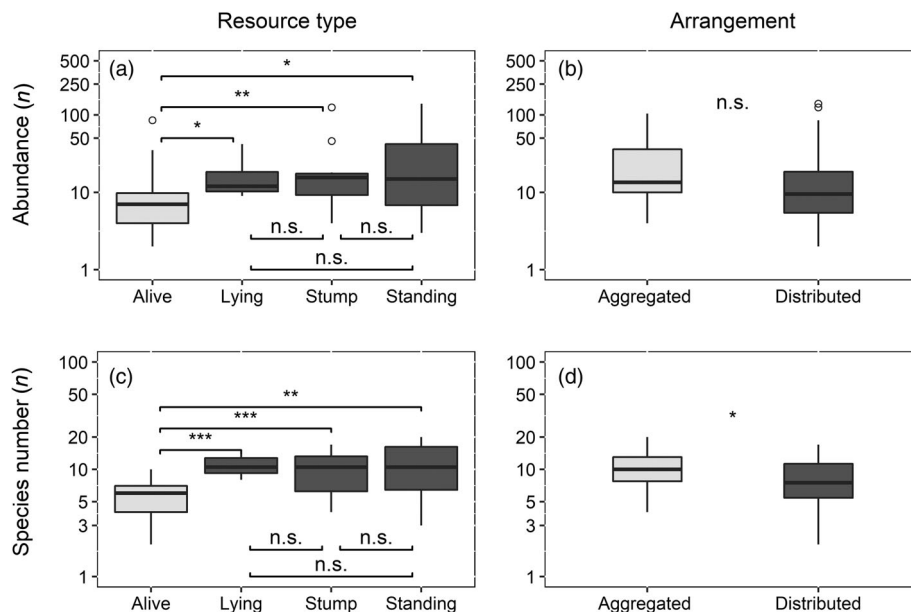


Fig. 2. Effects of resource type and deadwood arrangement on abundance and species number of colonising saproxylic beetles. Abundance and number of species of colonising saproxylic beetles (a, c) of different resource types (alive tree, lying deadwood, stump deadwood, standing deadwood) and (b, d) of the two different deadwood arrangements (aggregated, distributed). Significance codes above and under the boxplots indicate significant differences according to the fitted mixed effect model and the pairwise comparison of means (Tukey), respectively. Significance codes: *** ≤ 0.001 ; ** ≤ 0.01 ; * ≤ 0.05 . Note log scaled y-axis.

Table 1. Effects of resource type, resource arrangement and vertical position on the community composition of saproxylic beetles (Bray–Curtis dissimilarity, ADONIS analyses). Next to overall effects pairwise comparisons between resource type (alive tree, lying deadwood, stump deadwood, standing deadwood) and vertical position (bottom, middle, top) were presented. Differences in the community composition of beetle along the vertical position were investigated for alive trees and standing deadwood separately. Bold values indicate significance ($P < 0.05$).

Comparison	Variable	<i>F</i> statistic	Partial R^2	Adj. <i>P</i> -value
Resource type and deadwood arrangement				
Overall	Resource type	1.518	0.114	0.013
	Arrangement	0.502	0.013	0.975
Alive vs. lying deadwood	Resource type	2.147	0.109	0.022
	Arrangement	0.583	0.030	0.975
Alive vs. standing deadwood	Resource type	0.940	0.050	0.975
	Arrangement	0.971	0.051	0.975
Alive vs. stump deadwood	Resource type	1.107	0.059	0.975
	Arrangement	0.532	0.029	0.975
Lying deadwood vs. standing deadwood	Resource type	2.152	0.108	0.013
	Arrangement	0.821	0.041	0.975
Lying deadwood vs. stump deadwood	Resource type	1.864	0.093	0.022
	Arrangement	1.249	0.062	0.975
Standing deadwood vs. stump deadwood	Resource type	1.076	0.058	0.975
	Arrangement	0.473	0.026	0.975
Vertical position: alive tree				
Overall	Vertical position	0.994	0.080	0.661
Bottom vs. middle	Vertical position	1.082	0.063	0.661
Bottom vs. top	Vertical position	1.110	0.065	0.661
Middle vs. top	Vertical position	0.767	0.052	0.673
Vertical position: standing deadwood				
Overall	Vertical position	2.455	0.159	0.004
Bottom vs. middle	Vertical position	1.146	0.060	0.186
Bottom vs. top	Vertical position	4.262	0.200	0.009
Middle vs. top	Vertical position	2.363	0.122	0.022

all other deadwood types and marginal difference between lying deadwood and alive trees (Table 1).

The indicator analysis identified the families Staphylinidae and Cerylonidae with a significant indicator value for lying deadwood (Table S5). The family Monotomidae was associated with standing deadwood. The family characteristic for stump deadwood was Cantharidae (Table S5).

Effect of deadwood arrangement on the colonisation process of saproxylic beetles

The mixed-effect models showed no statistically significant effect of deadwood arrangement on the abundance of colonising saproxylic beetles. In contrast, species number was on average 25% higher in samples originating from aggregated compared to distributed deadwood arrangement (Fig. 2; Table S2). For species diversity, however, overlapping confidence intervals of the accumulation curves of aggregated and distributed deadwood arrangement indicated no significant differences for all values of q (Fig. 4 and S1; Table S4). Furthermore, no effect of the deadwood arrangement on the community composition of colonising saproxylic beetles were detected, nor could be found any association of families with a specific deadwood arrangement (Tables 1 and S5).

Differences between vertical position in host selection of saproxylic beetles

The mixed models indicate that there was a similar pattern of vertical stratification of host-seeking saproxylic beetles on alive trees and standing deadwood (Fig. 3). Abundance of saproxylic beetles was generally higher on traps at the bottom section of the trunk (Fig. 3; Table S3). Traps attached to the bottom section of the trunk on alive trees and standing deadwood caught on average ~433% and ~252% more individuals than the traps attached to the middle and top section, respectively (Fig. 3; Table S3). Similarly, traps attached to the bottom section of the trunk on alive trees and standing deadwood captured on average 100% and ~144% more species than the traps attached to the middle and top section, respectively (Fig. 3; Table S3). Differences between the vertical position in terms of species diversity estimates were more pronounced for standing deadwood than alive trees (Fig. 4 and S1; Table S4). Species richness and species diversity was estimated to be highest on the bottom section of standing deadwood, followed by the middle section and the top position (Fig. 4). The species accumulation curves based on the samples from middle and top positions show increasing divergence from $q = 0$ to $q = 2$ (Fig. S1). Thus, higher species diversity of the middle compared to the top position is predominantly driven by dominant species ($q = 2$). The effect of the vertical position on the community composition differed

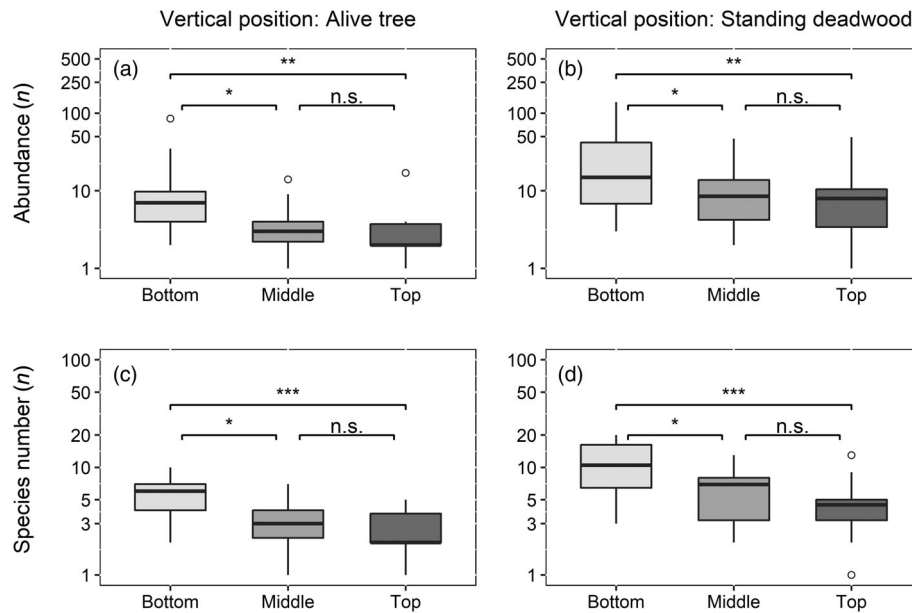


Fig 3. Effect of vertical position on abundance and number of species of colonising saproxylic beetles. Abundance and number of species of colonising saproxylic beetles (a, c) of three different vertical position on alive trees (bottom, middle, top) and (b, d) of three different vertical position on standing deadwood (bottom, middle, top). Significance codes above and under the boxplots indicate significant differences according to the fitted mixed effect model and the pairwise comparison of means (Tukey), respectively. Significance codes: *** ≤ 0.001 ; ** ≤ 0.01 ; * ≤ 0.05 . Note log scaled y-axis.

depending on the resource type considered. The analysis of the variances showed no influence of the vertical position on the beetle community on alive trees (Table 1). In contrast, significant different communities between the bottom and top section and the middle and top section could be found for standing deadwood, with Monotomidae having a significant indicator value for the bottom section of the trunk of standing deadwood (Tables 1 and S5).

Discussion

Colonisation of deadwood by saproxylic beetles

By sampling different deadwood types (lying, standing and stump deadwood) and alive trees, we addressed the question whether saproxylic host-seeking beetles are able to detect their preferred habitat before their arrival on the potential hosts. The analysis showed that all three deadwood types comprised higher abundances, species number and species diversity of colonising saproxylic beetles compared to alive trees. Consequently, our results suggest that saproxylic beetles identify suitable deadwood habitats prior landing, supporting the *primary attraction hypothesis* (Anderson, 1977; Tunset *et al.*, 1993; Brattli *et al.*, 1998). The abundance and number of species among the three deadwood types did not differ. However, resource type had a significant effect on the species community with a distinct species assemblage on lying deadwood compared to other deadwood types and alive trees.

Our findings are consistent with other studies, that investigated the host detection mechanism of saproxylic beetles using

traps baited with billets of the species' host tree (Tunset *et al.*, 1993; Brattli *et al.*, 1998) and thus, supporting the primary attraction hypothesis. In general, insects perceive their environment through processing of olfactory and gustatory signals. For some saproxylic species host selection is based on 'visual-olfactory synergism', albeit the interaction of cues reaches different degrees dependent on taxa and/or feeding guilds (Campbell & Borden, 2009). Nevertheless, VOC are a key facilitator in host selection mediating a positive response of saproxylic beetles to deadwood (Allison *et al.*, 2004). VOC are host-specific and their composition and emission rates change with ongoing decomposition and vary due to biotic and abiotic influences such as fungal or microbial attack or climatic factors (Holighaus *et al.*, 2007; Holighaus, 2012; Leather *et al.*, 2014).

While our results show that saproxylic beetles visited deadwood resources twice as often than alive trees, in terms of individuals and species, a subset of the species assemblage nonetheless landed on alive trees as well. Since there are no differences in the species composition between alive trees and deadwood in general, the host seeking appears to be random up to a certain degree. Several studies provide empirical support for the random-landing of saproxylic beetles by recording the same abundances of bark beetles on vertical stems of hosts and non-hosts (Berryman & Ashraf, 1970; Moeck *et al.*, 1981). However, it is assumed that the high concentration of olfactory cues originating from different sources which are in close vicinity one to each other affects the accuracy of short-range host recognition resulting in even distributions of individuals between hosts and non-hosts (Saint-Germain *et al.*, 2007). Accordingly, our study also underlines that the primary attraction and random landing hypotheses are not mutually exclusive.

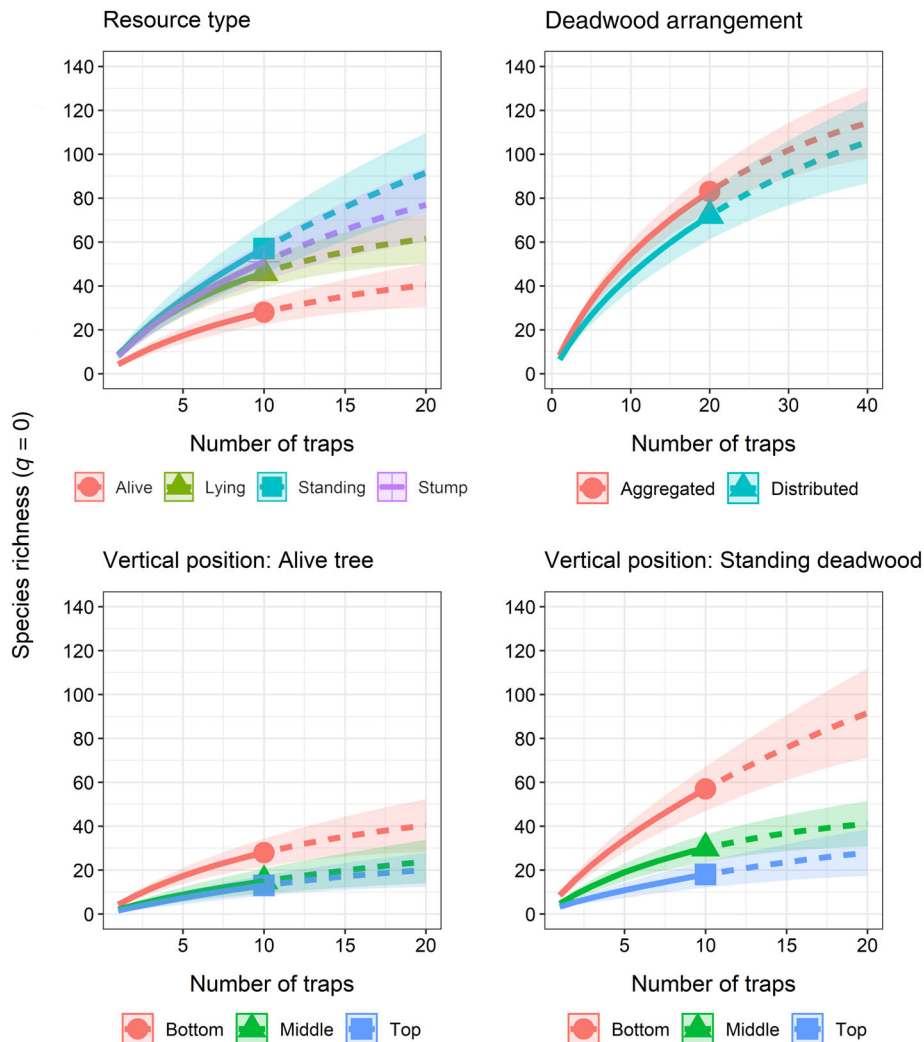


Fig 4. Rarefaction/extrapolation curves. Sample-based rarefaction (solid lines) and extrapolation (dashed lines) of colonising saproxylic beetle species richness (Hill number of order $q = 0$) with 95% confidence intervals (shaded area). Comparison of interpolated/extrapolated species richness among different resource types (alive tree, lying deadwood, stump deadwood, standing deadwood), deadwood arrangements (aggregated and distributed) and three different vertical positions separated for alive trees and standing deadwood (bottom = 0.5 m, middle = 4, top = 7.30–11.60 m). Analysis of the effect of resource type and deadwood arrangement on species richness is based on traps attached to the bottom section of alive trees and standing deadwood, stump and lying deadwood.

Our results suggest that host-seeking saproxylic beetles are able to differentiate between lying deadwood and standing or stump deadwood before their arrival. It is known that different deadwood types support different species assemblages (Jonsell & Weslien, 2003; Gibb *et al.*, 2006; Hedgren, 2007; Hjältén *et al.*, 2010; Bouget *et al.*, 2012; Müller *et al.*, 2013). The pattern that emerges in relation to the species compositions on standing and lying deadwood (Gibb *et al.*, 2006; Bouget *et al.*, 2012) or on standing and lying deadwood as well as stump deadwood (Hjältén *et al.*, 2010) are more precisely defined in studies that investigate beetle emergence compared to our study focusing on colonisation. Consequently, this might indicate that the filtering effect on species composition (which results from species specialisation) acts on several levels—species that land

on the object versus species that can develop successfully there. Hence, the filter on species assemblages becomes stronger towards the successful development of individuals within deadwood.

The difference in species compositions is probably due to different water-temperature regimes among the deadwood types, with higher moisture content and smaller temperature fluctuations in lying deadwood compared to standing deadwood (Pouska *et al.*, 2016), which results in different fungal communities (Lindhe *et al.*, 2004; Pouska *et al.*, 2016; Pasanen *et al.*, 2019). Since many species of saproxylic invertebrates feed on fungi in decaying wood (Stokland *et al.*, 2012), it appears obvious that the distinct species community of fungi in lying deadwood is also reflected in the community of saproxylic

beetles. Hence, host detection of lying deadwood might be partly explained by different fungal assemblages and thus, by emissions of distinct VOC profiles to which fungi can contribute (Leather *et al.*, 2014). Moreover, factors such as the missing root connection to the soil of lying deadwood might accelerate the decomposition (Jakuš, 1998), making them, at least during the first years of decay, a more suitable habitat than standing and stump deadwood, which might be able to defend themselves longer against fungi and insects. Sticky traps are a proper passive sampling system to access species landing or crawling on deadwood object of different properties. However, the overall small sample sizes compared to other insect trapping methods (e.g., flight interception traps, emergence traps) for saproxylic beetles did not allow additional analyses of subsets (e.g., families or feeding guilds) of our entire dataset. Furthermore, it is also noticeable that larger beetle species are nearly absent from the samples which might indicate that they have managed to escape from the sticky traps. Albeit the utilisation of a consistent sampling system made it possible to test hypotheses regarding differences between the sampled catches, this might be a limitation of the method worth considering in future application. Although this study cannot compressively and in detail reveal the entire process of deadwood colonisation by saproxylic beetles and particular the mechanisms behind connected to chemocology stays largely unresolved, it shows that the biodiversity pattern can also be found during the colonisation process.

Open canopy increases diversity of host-seeking saproxylic beetles

Our study design with aggregated and distributed deadwood arrangement is concomitant with two factors which might influence the colonisation process of saproxylic beetles. Both the accumulation of deadwood in groups (aggregated arrangement) and the concomitant higher degree of sun exposure on the plots were expected to increase abundance and species number. Additionally, we anticipated a change in species composition. Our results revealed that aggregated deadwood arrangement with the concomitant canopy openness had a positive effect on species number but not on abundance of host-seeking saproxylic beetles. Species diversity was found to be higher on plots with open canopy, albeit not significant. However, canopy openness, which was used as a surrogate for microclimate, had no effect on the species composition of saproxylic beetles.

The degree of sun exposure on deadwood influences species composition of saproxylic beetles colonising deadwood (Lindhe *et al.*, 2005; Johansson *et al.*, 2006; Vodka *et al.*, 2009; Seibold *et al.*, 2016; Joelsson *et al.*, 2018). This effect is probably due the prevailing microclimatic conditions on stand level and deadwood objects. On the one hand, canopy openness mediates higher maximum temperatures and lower humidity near the ground (Joelsson *et al.*, 2018), on the other hand, it increases annual evaporation rates of deadwood due to the higher sun exposure (Lindhe *et al.*, 2005). We expected that the effect of sun exposure would also be reflected in the pattern of host-seeking saproxylic beetles. However, our results revealed that

deadwood under closed canopy exhibits rather a subset of the species assemblage of deadwood under open canopy, which implies that sun exposed deadwood does not bear a different species community of host-seeking saproxylic beetles. Nevertheless, the species number was found to be higher on plots with aggregated arrangement of deadwood. This might be explained by the higher degree of sun exposure, which has been found to be a main driver of saproxylic beetle species richness (Ranius & Jansson, 2000; Lindhe *et al.*, 2005; Vodka *et al.*, 2009). In contrast to our expectations, abundance remained unaffected by the arrangement of deadwood and/or the canopy openness. In contrast, studies using flight intercept traps demonstrated that deadwood exposed to sunny conditions exhibit higher abundance (Seibold *et al.*, 2016). However, at this point, it has to be stressed that different sampling techniques only allow narrow conclusion. It is possible that different scales of saproxylic beetles' behaviour, in particular the activity, colonisation process or colonisation success, reflect different patterns among different microclimatic conditions. Consequently, it is probable that the significant higher species richness on plots with aggregated deadwood arrangement is not an effect of generally more activity in open canopy areas but reflects habitat preferences.

Second, besides sun exposure, the arrangement of deadwood might also play an important role in host discrimination. Standing and lying deadwood as well as stump deadwood grouped in a more open area might be easier to detect olfactory and/or visually by host-seeking beetles than scattered within dense forest (Sverdrup-Thygeson & Ims, 2002; Saint-Germain *et al.*, 2007). In addition, colonisation of deadwood in open areas might also be easier for beetles, whose dispersal is facilitated by wind (Sverdrup-Thygeson & Ims, 2002). Nonetheless, in this study no differences in capture rates among deadwood arrangements could be detected. This is consistent with an experiment where canopy cover was kept constant and no significant difference in terms of abundance between standing deadwood in aggregated and distributed arrangement (except for Scolytinae during one sampling period) could be found (Dufour-Pelletier *et al.*, 2020).

Vertical stratification of host-seeking saproxylic beetles on resources

A vertical distribution pattern on standing resources (i.e., standing deadwood and alive trees) in terms of abundance, number of species, species richness or species composition indicates that beetles are able to detect the different prevailing microclimatic conditions between different heights. Our results suggest that there is vertical stratification on both, alive trees and standing deadwood, with significantly higher abundance and species number of saproxylic beetles at the bottom sections (0.5 m above ground). Species richness and diversity decreases with increasing trap height, that is, trunk sections. In contrast to alive trees, there is an effect of vertical position on the species composition of standing deadwood with different community compositions between bottom and top positions and middle and top positions of traps.

Vertical stratification of saproxylic beetle communities between canopy and ground-level in forests is well established

through previous research, albeit no consistent pattern can be revealed for the general abundance or species richness (Ulyshen & Hanula, 2007; Bouget *et al.*, 2011; Maguire *et al.*, 2014; Holdsworth *et al.*, 2016; Weiss *et al.*, 2016). Focusing on the vertical distribution during the colonisation process of hosts, this study found stratification of saproxylic beetles in respect of abundance and species number on standing deadwood and alive trees, but different species compositions between heights only on standing deadwood. This result is partly consistent with the findings of Horn *et al.* (2020), who found higher abundances of beetles occupying the lower section of the trunk. However, in earlier studies diverging patterns have been observed, which might arise from different species communities belonging to different guilds, but also forest structure, composition or management practices and its influence on layer-specific microclimatic conditions (Weiss *et al.*, 2016; Berkov, 2018; Ulyshen & Sheehan, 2019). Moreover, it has to be stressed that the pattern of general activity (obtained by samples from flight intercept traps), the colonisation process (obtained by sticky traps) or colonisation success (obtained by rearing) do not necessarily have to correspond to a common pattern of vertical stratification. For instance, we cannot eliminate the possibility that saproxylic beetles land on standing deadwood, irrespective the association of habitat preferences and stem sections, and find their favoured trunk section by moving up or down the stem. However, taking in consideration that predators were observed to actively search for prey by crawling up and down the trunk (Hanula & Franzreb, 1998), the assessment of potential habitats by saproxylic beetles prior landing appears plausible, because it reduces time spend seeking and thus minimises opportunity costs and predation risk (Pyke *et al.*, 1977). Besides, it is likely that some epigeal saproxylic species crawled onto the resources from the forest floor and were subsequently captured by the traps on the bottom section of the stem, consequently leading to higher abundance and species richness. Nonetheless, high predation pressure near the ground (Šipoš *et al.*, 2013) leads to the assumption that only species specialised on conditions characterising the lower part of the trunk would risk to land or crawl on parts close to the ground.

While the pattern of vertical stratification was similar on alive trees and standing deadwood in terms of abundance and species diversity, this does not apply for changes in species assemblages. Consequently, we assume that saproxylic beetles approach standing deadwood more specifically, that is, according to their habitat preferences. This can probably be explained by the beetles specialisation on different microclimatic conditions which differ vertically on standing deadwood (Abrahamsson & Lindbladh, 2006; Sheehan *et al.*, 2019). Sticky traps attached at the top position recorded less individuals and species and a different community, which is probably due to the drier conditions of higher sections mediated by higher exposure to the sun and wind (Shaw, 2004; Abrahamsson & Lindbladh, 2006; Sheehan *et al.*, 2019). The decreasing diameter, that is, the decreasing ratio of surface and volume, intensifies the effect of sun and wind (Lachat *et al.*, 2013). The microclimatic conditions inside the trunk directly affect the composition of wood-inhabiting fungi community, which therefore differs between higher and lower sections of the trunk (Levy, 1982; Heilmann-Clausen, 2001).

Practical implications for forest nature conservation

A better understanding of biodiversity patterns can help to better protect and promote species diversity. Our study shows that species diversity increases with habitat heterogeneity. It highlights the value of different types of deadwood, especially standing deadwood, for the diversity saproxylic beetles and hence supports the recommendation to integrate more standing deadwood into forestry measures. We also advocate for the provision of deadwood in both open and closed canopy cover since it may support a considerable proportion of the diversity of saproxylic beetles. For future research, it may be of interest to measure atmospheric VOC concentrations emitted from different deadwood types and under different environmental conditions in order to explore their direct effects on biodiversity patterns. The knowledge about the host colonisation by saproxylic beetles enables us to specifically promote groups of saproxylic beetles, whose habitats are most threatened by forestry, by creating diversified deadwood habitats in managed forests. For instance, whereas the provision of lying deadwood benefits rove beetles (Staphylinidae) and minute bark beetles (Cerylonidae), stump deadwood supports the family of soldier beetles (Cantharidae) and standing deadwood Monotomidae.

Acknowledgements

This research was supported by the project 'BioHolz' (grant no. 01LC1323A) in the funding program 'Research for the Implementation of the National Biodiversity Strategy (F&U NBS)' of the German Federal Ministry for Education and Research (BMBF) and the German Federal Agency for Nature Conservation (BfN), with funds provided by the German Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU). We would like to thank the Bavarian Forest National Park administration and the employees for their support and valuable assistance, as well as our colleagues from the internship for the great cooperation in the data collection. We are also very grateful to Carina Niggel for illustrating the figure showing our study design.

Conflict of interests

The authors declare they have no conflict of interests.

Author Contributions

MG and JH developed the idea of the manuscript. JH and JM designed the experiment. MG and JH collected the data. MG and JH analyzed the data. MG led the writing of the manuscript. JH supervised the project. All authors interpreted the results, contributed to writing and gave final approval for publication of the submitted manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting Information

References

- Abrahamsson, M. & Lindbladh, M. (2006) A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (*Picea abies*). *Forest Ecology and Management*, **226**, 230–237. <https://doi.org/10.1016/j.foreco.2006.01.046>.
- Alinvi, O., Ball, J.P., Danell, K., Hjalten, J., & Pettersson, J.B. (2007) Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. *Journal of Insect Conservation*, **11**, 99–112. <https://doi.org/10.1007/s10841-006-9012-2>.
- Allison, J.D., Borden, J.H. & Seybold, S.J. (2004) A review of the chemical ecology of the Cerambycidae (Coleoptera). *Chemoecology*, **14**, 123–150. <https://doi.org/10.1007/s00049-004-0277-1>.
- Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46. <https://doi.org/10.1046/j.1442-9993.2001.01070.x>.
- Anderson, R.F. (1977) Dispersal and attack behavior of the southern pine engraver, *Ips grandicollis* Eichh., Coleoptera, Scolytidae. *Insect Ecology* (ed. by H.M. Kuhlman & H.C. Chiang), pp. 17–23. Minnesota Agricultural Experiment Station, Technical Bulletin 310, Minneapolis.
- Baayen, H. (2012) Mixed-effects models. *The Oxford Handbook of Laboratory Phonology* (ed. by A.C. Cohn, C. Fougerson and M.K. Huffman), pp. 668–677. Oxford University Press, Oxford.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B*, **57**, 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.
- Berkov, A. (2018) Seasonality and stratification: neotropical saproxylic beetles respond to a heat and moisture continuum with conservatism and plasticity. *Saproxylic Insects*. (ed. by M.D. Ulyshen), pp. 547–578. Springer, Cham, Switzerland.
- Berryman, A.A. & Ashraf, M. (1970) Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera: Scolytidae). *Canadian Entomologist*, **102**, 1229–1236.
- Bouget, C., Brin, A. & Brustel, H. (2011) Exploring the “last biotic frontier”: are temperate forest canopies special for saproxylic beetles? *Forest Ecology and Management*, **261**, 211–220. <https://doi.org/10.1016/j.foreco.2010.10.007>.
- Bouget, C., Nusillard, B., Pineau, X. & Ricou, C. (2012) Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. *Insect Conservation and Diversity*, **5**, 264–278. <https://doi.org/10.1111/j.1752-4598.2011.00160.x>.
- Brattli, J.G., Andersen, J. & Nilssen, A.C. (1998) Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. *Journal of Applied Entomology*, **122**, 345–352. <https://doi.org/10.1111/j.1439-0418.1998.tb01511.x>.
- Campbell, S.A. & Borden, J.H. (2006) Close-range, in-flight integration of olfactory and visual information by a host-seeking bark beetle. *Entomologia Experimentalis et Applicata*, **120**, 91–98. <https://doi.org/10.1111/j.1570-7458.2006.00425.x>.
- Campbell, S.A. & Borden, J.H. (2009) Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. *Oikos*, **118**, 553–563. <https://doi.org/10.1111/j.1600-0706.2009.16761.x>.
- Chao, A., Chiu, C.-H. & Jost, L. (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 297–324. <https://doi.org/10.1146/annurev-ecolsys-120213-091540>.
- Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533–2547. <https://doi.org/10.1890/11-1952.1>.
- Collins, C.S., Conner, R.N. & Saenz, D. (2002) Influence of hardwood midstory and pine species on pine bole arthropods. *Forest Ecology and Management*, **164**, 211–220. [https://doi.org/10.1016/S0378-1127\(01\)00595-3](https://doi.org/10.1016/S0378-1127(01)00595-3).
- De Frenne P., Zellweger F., Rodríguez-Sánchez F., Scheffers B., Hylander K., Luoto M., Vellend M., Verheyen K., & Lenoir J. (2019) Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, **3**, 744–749. <https://doi.org/10.1038/s41559-019-0842-1>.
- Dufour-Pelletier S., Tremblay J. A., Hébert C., Lachat T., & Ibarzabal J. (2020) Testing the Effect of Snag and Cavity Supply on Deadwood-Associated Species in a Managed Boreal Forest. *Forests*, **11**, 424. <https://doi.org/10.3390/f11040424>.
- Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366. <https://doi.org/10.2307/2963459>.
- Eichholz, M.W., Zari, E.C. & Sierzega, K.P. (2019) Quantifying corticolous arthropods using sticky traps. *Journal of Visualized Experiments*, **2020**, 1–6. <https://doi.org/10.3791/60320>.
- Forrester, J.A., Mladenoff, D.J., Gower, S.T. & Stoffel, J.L. (2012) Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. *Forest Ecology and Management*, **265**, 124–132. <https://doi.org/10.1016/j.foreco.2011.10.038>.
- Gibb H., Pettersson R.B., Hjalten J., Hilszczański J., Ball J.P., Johansson T., Atlegrim O., & Danell K. (2006) Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biological Conservation*, **129**, 437–450. <https://doi.org/10.1016/j.biocon.2005.11.010>.
- Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1–23. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150507>.
- Hanula, J.L. & Franzreb, K. (1998) Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. *Forest Ecology and Management*, **102**, 89–102. [https://doi.org/10.1016/S0378-1127\(97\)00119-9](https://doi.org/10.1016/S0378-1127(97)00119-9).
- Hedgren, P.O. (2007) Early arriving saproxylic beetles (Coleoptera) and parasitoids (Hymenoptera) in low and high stumps of Norway spruce. *Forest Ecology and Management*, **241**, 155–161. <https://doi.org/10.1016/j.foreco.2007.01.020>.

- Heilmann-Clausen, J. (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. *Mycological Research*, **105**, 575–596. <https://doi.org/10.1017/S0953756201003665>.
- Hjältén, J., Stenbacka, F. & Andersson, J. (2010) Saproxyllic beetle assemblages on low stumps, high stumps and logs: implications for environmental effects of stump harvesting. *Forest Ecology and Management*, **260**, 1149–1155. <https://doi.org/10.1016/j.foreco.2010.07.003>.
- Holdsworth, S., Hammond, P.M. & Eggleton, P. (2016) Assessing high compositional differences of beetle assemblages across vertical woodland strata in the New Forest, Hampshire, England. *Journal of Natural History*, **50**, 2477–2485. <https://doi.org/10.1080/00222933.2016.1195022>.
- Holighaus, G. (2012) *Odour signals relevant to beetles in deadwood habitats - odorants, olfaction and behaviour*. PhD thesis, Fakultät für Forstwissenschaften und Waldökologie, Georg-August-Universität, Göttingen.
- Holighaus, G. & Schütz, S. (2006) Odours of wood decay as semiochemicals for *Trypodendron domesticum* L. (Col., Scolytidae). *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie*, **15**, 161–166.
- Holighaus, G., Thakeow, P. & Schütz, S. (2007) Volatile organic compounds for wood assessment. *Wood Production, Wood Technology, and Biotechnological Impacts*. (ed. by U. Kües), pp. 197–228. Universitätsverlag Göttingen, Göttingen, Germany.
- Horn, S., Hanula, J.L. & Ulyshen, M.D. (2020) Arthropod abundance and biomass in response to *Pinus taeda* L. Trunk Height. *Journal of Entomological Science*, **55**, 171–187. <https://doi.org/10.18474/0749-8004-55.2.171>.
- Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Hsieh, T.C., Ma, K.H., & Chao, A. (2019) iNEXT: interpolation and extrapolation for species diversity. R-project.
- Hynum, B.G. & Berryman, A.A. (1980) *Dendroctonus ponderosae* (Coleoptera: Scolytidae): pre-aggregation landing and gallery initiation on lodgepole pine. *Canadian Entomologist*, **112**, 185–191.
- Jakuš, R. (1998) Patch level variation of bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic condition: proportions of colonized surface and variability of ecological conditions. *Journal of Applied Entomology*, **122**, 543–546. <https://doi.org/10.1111/j.1439-0418.1998.tb01541.x>.
- Joelsson, K., Hjältén, J. & Work, T. (2018) Uneven-aged silviculture can enhance within stand heterogeneity and beetle diversity. *Journal of Environmental Management*, **205**, 1–8. <https://doi.org/10.1016/j.jenvman.2017.09.054>.
- Johansson T., Gibb H., Hilszczański J., Pettersson R.B., Hjältén J., Atlegrim O., Ball J.P., & Danell K. (2006) Conservation-oriented manipulations of coarse woody debris affect its value as habitat for spruce-infesting bark and ambrosia beetles (Coleoptera: Scolytinae) in northern Sweden. *Canadian Journal of Forest Research*, **36**, 174–185. <https://doi.org/10.1139/x05-235>
- Jonsell, M. & Weslien, J. (2003) Felled or standing retained wood—it makes a difference for saproxyllic beetles. *Forest Ecology and Management*, **175**, 425–435. [https://doi.org/10.1016/S0378-1127\(02\)00143-3](https://doi.org/10.1016/S0378-1127(02)00143-3).
- Jonsson, B.G. & Stokland, J.N. (2012) The surrounding environment. *Biodiversity in Dead Wood*. (ed. by J.N. Stokland, J. Siitonen and B. G. Jonsson), pp. 194–217. Cambridge University Press, Cambridge, UK.
- Kermavnar J., Ferlan M., Marinšek A., Eler K., Kobler A., & Kutnar L. (2020) Effects of various cutting treatments and topographic factors on microclimatic conditions in Dinaric fir-beech forests. *Agricultural and Forest Meteorology*, **295**, 108186. <https://doi.org/10.1016/j.agrfor.met.2020.108186>
- Koban M.B., Gossner M.M., Müller J., Steidle J.L.M., Bässler C., Hothorn T., Unsicker S.B., & Seibold S. (2016) Short-distance attraction of saproxyllic Heteroptera to olfactory cues. *Insect Conservation and Diversity*, **9**, 254–257. <https://doi.org/10.1111/icad.12161>
- Lachat, T., Bouget, C., Büttler, R. & Müller, J. (2013) Deadwood: quantitative and qualitative requirements for the conservation of saproxyllic biodiversity. *Integrative Approaches as an Opportunity for the Conservation of forest Biodiversity*. (ed. by D. Kraus and F. Krumm), pp. 92–102. European Forest Institute, Freiburg.
- Leather, S.R., Baumgart, E.A., Evans, H.F. & Quicke, D.L.J. (2014) Seeing the trees for the wood - beech (*Fagus sylvatica*) decay fungal volatiles influence the structure of saproxyllic beetle communities. *Insect Conservation and Diversity*, **7**, 314–326. <https://doi.org/10.1111/icad.12055>.
- Levy, J.F. (1982) The place of basidiomycetes in the decay of wood in contact with the ground. *Decomposer Basidiomycetes: Their Biology and Ecology*. (ed. by J. Frankland, J. Hedger and M. Swift), pp. 161–178. Cambridge University Press, Cambridge, UK.
- Lindhe, A., Åsenblad, N. & Toresson, H.G. (2004) Cut logs and high stumps of spruce, birch, aspen and oak - nine years of saproxyllic fungi succession. *Biological Conservation*, **119**, 443–454. <https://doi.org/10.1016/j.biocon.2004.01.005>.
- Lindhe, A., Lindelöw, Å. & Åsenblad, N. (2005) Saproxyllic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation*, **14**, 3033–3053. <https://doi.org/10.1007/s10531-004-0314-y>.
- Maguire D.Y., Robert K., Brochu K., Larrivière M., Buddle C.M., & Wheeler T.A. (2014) Vertical Stratification of Beetles (Coleoptera) and Flies (Diptera) in Temperate Forest Canopies. *Environmental Entomology*, **43**, 9–17. <https://doi.org/10.1603/en13056>
- Mayfield, A.E. & Brownie, C. (2013) The redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) uses stem silhouette diameter as a visual host-finding cue. *Environmental Entomology*, **42**, 743–750. <https://doi.org/10.1603/EN12341>.
- Moeck, H.A., Wood, D.L. & Lindahl, K.Q. (1981) Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicornis*. *Journal of Chemical Ecology*, **7**, 49–83. <https://doi.org/10.1007/BF00988635>.
- Müller J., Brunet J., Brin A., Bouget C., Brustel H., Bussler H., Förster B., Isacson G., Köhler F., Lachat T., & Gossner M.M. (2013) Implications from large-scale spatial diversity patterns of saproxyllic beetles for the conservation of European Beech forests. *Insect Conservation and Diversity*, **6**, 162–169. <https://doi.org/10.1111/j.1752-4598.2012.00200.x>
- Müller, J. & Goßner, M.M. (2010) Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxyllic beetles. *Biological Conservation*, **143**, 625–633. <https://doi.org/10.1016/j.biocon.2009.11.027>.
- Müller, J., Noss, R.F., Bussler, H. & Brandl, R. (2010) Learning from a “benign neglect strategy” in a national park: Response of saproxyllic beetles to dead wood accumulation. *Biological Conservation*, **143**, 2559–2569. <https://doi.org/10.1016/j.biocon.2010.06.024>.
- Müller J., Ulyshen M., Seibold S., Cadotte M., Chao A., Bässler C., Vogel S., Haggé J., Weiß I., Baldrian P., Tláškal V., & Thorn S. (2020) Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, **129**, 1579–1588. <https://doi.org/10.1111/oik.07335>
- Musco, A., Bagnato, S., Sidari, M. & Mercurio, R. (2014) A review of the roles of forest canopy gaps. *Journal of Forest Research*, **25**, 725–736. <https://doi.org/10.1007/s11676-014-0521-7>.

- Pasanen, H., Juutilainen, K. & Siitonen, J. (2019) Responses of polypore fungi following disturbance-emulating harvesting treatments and deadwood creation in boreal Norway spruce dominated forests. *Scandinavian Journal of Forest Research*, **34**, 557–568. <https://doi.org/10.1080/02827581.2019.1663915>.
- Pouska, V., Macek, P. & Zibarová, L. (2016) The relation of fungal communities to wood microclimate in a mountain spruce forest. *Fungal Ecology*, **21**, 1–9. <https://doi.org/10.1016/j.funeco.2016.01.006>.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, **52**, 137–154. <https://doi.org/10.1086/409852>.
- Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, **95**, 85–94. [https://doi.org/10.1016/S0006-3207\(00\)00007-0](https://doi.org/10.1016/S0006-3207(00)00007-0).
- Roberts, D.W. (2019) labdsv: ordination and multivariate analysis for ecology. R package version 2.0-1.
- Saint-Germain, M., Buddle, C.M. & Drapeau, P. (2007) Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? *Agricultural and Forest Entomology*, **9**, 227–235. <https://doi.org/10.1111/j.1461-9563.2007.00337.x>.
- Saint-Germain, M., Buddle, C.M. & Drapeau, P. (2006) Sampling saproxylic Coleoptera: scale issues and the importance of behavior. *Environmental Entomology*, **35**, 478–487. <https://doi.org/10.1603/0046-225X-35.2.478>.
- van Schmidl, J. & Bußler, H. (2004) Ökologische Gilden xylobionter Käfer Deutschlands. *Naturschutz und Landschaftsplan*, **36**, 202–218.
- Seibold S., Bässler C., Baldrian P., Thorn S., Müller J., & Gossner M.M. (2014) Wood resource and not fungi attract early-successional saproxylic species of Heteroptera -an experimental approach. *Insect Conservation and Diversity*, **7**, 533–542. <https://doi.org/10.1111/icad.12076>
- Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., & Müller J. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, **53**, 934–943. <https://doi.org/10.1111/1365-2664.12607>
- Shaw, D.C. (2004) Vertical organization of canopy biota. *Forest Canopies*. (ed. by M.D. Lowman and H.B. Rinker), pp. 73–101. Elsevier Academic Press, San Diego, California.
- Sheehan, T.N., Ulyshen, M.D., Horn, S. & Hoebcke, E.R. (2019) Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection? *Journal of Pest Science*, **92**(2004), 327–341. <https://doi.org/10.1007/s10340-018-1026-5>.
- Siitonen, J. & Stokland, J.N. (2012) Tree size. *Biodiversity in Dead Wood* (ed. by Stokland, J.N., Siitonen, J. & Jonsson, B.G.), pp. 183–193. Cambridge University Press, Cambridge, UK.
- Šipoš, J., Drozdová, M. & Drozd, P. (2013) Assessment of trends in predation pressure on insects across temperate forest microhabitats. *Agricultural and Forest Entomology*, **15**, 255–261. <https://doi.org/10.1111/afe.12012>.
- Speight, M.C.D. (1989) *Saproxylic Invertebrates and Their Conservation*. Council of Europe, Strasbourg.
- Stokland, J.N. (2012) Host-tree associations. *Biodiversity in Dead Wood* (ed. by Stokland, J.N., Siitonen, J. & Jonsson, B.G.), pp. 82–109. Cambridge University Press, Cambridge, UK.
- Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012) *Biodiversity in Dead Wood*. Cambridge University Press, Cambridge, UK.
- Strom, B.L., Roton, L.M., Goyer, R.A. & Meeker, J.R. (1999) Visual and semiochemical disruption of host finding in the southern pine beetle. *Ecological Applications*, **9**, 1028–1038. [https://doi.org/10.1890/1051-0761\(1999\)009\[1028:VASDOH\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1028:VASDOH]2.0.CO;2).
- Sverdrup-Thygeson, A. & Ims, R.A. (2002) The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation*, **108**, 377–378. [https://doi.org/10.1016/S0006-3207\(02\)00142-8](https://doi.org/10.1016/S0006-3207(02)00142-8).
- Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., & Seidl, R. (2020) Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agricultural and Forest Meteorology*, **291**, 108066. <https://doi.org/10.1016/j.agrformet.2020.108066>
- Tunset, K., Nilssen, A.C. & Andersen, J. (1993) Primary attraction in host recognition of coniferous bark beetles and bark weevils (Col., Scolytidae and Curculionidae). *Journal of Applied Entomology*, **115**, 155–169. <https://doi.org/10.1111/j.1439-0418.1993.tb00375.x>.
- Ulyshen, M.D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, **261**, 1479–1489. <https://doi.org/10.1016/j.foreco.2011.01.033>.
- Ulyshen, M.D. & Hanula, J.L. (2007) A comparison of the beetle (Coleoptera) fauna captured at two heights above the ground in a North American temperate deciduous forest. *The American Midland Naturalist*, **158**, 260–278. [https://doi.org/10.1674/0003-0031\(2007\)158\[260:ACOTBC\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2007)158[260:ACOTBC]2.0.CO;2).
- Ulyshen, M.D. & Sheehan, T.N. (2019) Trap height considerations for detecting two economically important forest beetle guilds in southeastern US forests. *Journal of Pest Science*, **92**(2004), 253–265. <https://doi.org/10.1007/s10340-017-0883-7>.
- Vodka, S., Konvicka, M. & Cizek, L. (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: Implications for forest history and management. *Journal of Insect Conservation*, **13**, 553–562. <https://doi.org/10.1007/s10841-008-9202-1>.
- Vuidot, A., Paillet, Y., Archaux, F. & Gosselin, F. (2011) Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, **144**, 441–450. <https://doi.org/10.1016/j.biocon.2010.09.030>.
- Weiss, M., Procházka, J., Schlaghamerský, J. & Cizek, L. (2016) Fine-scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: similar patterns despite low faunal overlap. *PLoS One*, **11**, e0149506. <https://doi.org/10.1371/journal.pone.0149506>.

Accepted 19 September 2021

Editor/associate editor: Raphael Didham