RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Dead wood distributed in different-sized habitat patches enhances diversity of saproxylic beetles in a landscape experiment

Elena Haeler[1,2,3,4] 🟢 | Jonas Stillhard[4] 🟢 | Karin Hindenlang Clerc[5] | Loïc Pellissier[3,4] 🟢 | Thibault Lachat[2,4] 🟢

[1]Department of Forest Growth, Silviculture and Genetics, Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), Vienna, Austria

[2]Forest Sciences, School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Zollikofen, Switzerland

[3]Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zurich, Switzerland

[4]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[5]Wildnispark Zurich Foundation, Sihlwald, Switzerland

Correspondence
Elena Haeler
Email: elena.haeler@bfw.gv.at

Funding information
Bundesamt für Umwelt

Handling Editor: Yolanda Wiersma

Abstract

1. Human intervention often alters the availability of habitat for biodiversity. The conservation of biodiversity therefore requires an optimized habitat management. In forests, dead wood represents one of the most important habitats and in boreal and temperate regions around 25% of forest species depend on it (= saproxylic species). Increasing the amount of dead wood in managed forests has thus become a policy objective, but there is no consensus on how to best distribute dead wood in space.

2. In a landscape experiment, we exposed freshly cut beech branches in bundles of different sizes (one, three, six and 12 branches) in the forest, representing newly created habitat patches to be colonized by saproxylic beetles. We investigated how species richness in a 'single large' branch bundle compares to that in 'several small' bundles (SLOSS debate). We further tested the effects of dead wood availability (amount and isolation) in the surrounding landscape (20–200 m) and environmental factors (temperature and light availability) on species richness, abundance and community composition.

3. The species richness of the pooled small bundles ($1 + 3 + 6 = 10$ branches) was as high as that of the large bundle (12 branches), despite having a smaller total surface, demonstrating the benefit of spatially dispersed habitat patches for total diversity. Also community composition differed and every bundle size yielded some unique species. Dead wood availability in the surrounding landscape had a minor effect in comparison. Our results further highlight the importance of microsite heterogeneity: species richness was related to light availability, and abundance and community composition were related to temperature.

4. *Synthesis and applications*: Larger amounts of dead wood harbour more saproxylic beetle species and the distribution of dead wood in patches of different sizes within the forest can promote the development of variable species communities. Combined, this results in a higher species diversity. In managed forests, where

retained dead wood is often homogeneous in terms of size or tree species, increasing heterogeneity by distributing dead wood in the forest could foster higher diversity of saproxylic species.

KEYWORDS

biodiversity, colonization, conservation, dead wood availability, forest management, habitat heterogeneity, saproxylic beetles, SLOSS

1 | INTRODUCTION

Habitat loss is one of the main drivers of declines in biodiversity (Brooks et al., 2002; Díaz et al., 2019; Wilcove et al., 1998). This loss of overall habitat is also associated with an increased fragmentation of the remaining habitat into smaller and more isolated patches. The size and distribution of habitat patches in the landscape could affect biodiversity independent of the total habitat amount with implications for biodiversity conservation (Fahrig, 2003, 2017; Hanski, 2015; Villard & Metzger, 2014). Conservation measures targeting biodiversity attempt to achieve the optimal distribution of habitat through its preservation or creation, for example, for optimizing biodiversity in sustainable forestry or agriculture systems (Bouget & Parmain, 2016; Mason & Zapponi, 2016; Tscharntke et al., 2012). In practice however, it remains difficult to disentangle distribution, patch sizes and total amount of habitat, as they are frequently intercorrelated (Fahrig, 2017).

For optimizing the spatial distribution of habitat, different theories and concepts explaining the relationship between biodiversity patterns and the availability of habitat in the landscape have been proposed. A central theory linking the distribution of habitats to biodiversity is the theory of island biogeography from MacArthur and Wilson (1967), which was later applied to conservation (Whittaker & Fernández-Palacios, 2007). It states that species richness on an island results from colonization and extinction processes and depends on its size and isolation. Like islands, fragmented terrestrial ecosystems can vary in size and levels of isolation (Fahrig, 2013; Tscharntke et al., 2012). Hence, applied to conservation, the theory of island biogeography raises the question whether a larger continuous habitat patch should be prioritized over many smaller patches, for example, for the establishment of protected areas (Diamond, 1975; Ovaskainen, 2002; Rösch et al., 2015; Tjørve, 2010; Tscharntke et al., 2012). In particular, the 'Single Large Or Several Small' (SLOSS) debate argued whether species richness of a single large habitat patch is higher than the species richness of several small accumulated patches (Diamond, 1975; Fahrig, 2020). Fahrig et al. (2022) propose mechanisms regarding extinction–colonization dynamics and beta diversity as driving forces. Empirical studies often show that when the same amount of habitat is compared, the accumulated smaller patches harbour more species than few larger ones (Fahrig, 2020; Rösch et al., 2015). This effect is often explained by a higher habitat heterogeneity of more patches, resulting in a higher species richness (Hutchinson, 1959; Rosenzweig & Abramsky, 1993). Comparing habitat patch sizes independent of heterogeneity to determine most efficient strategies to manage habitat distribution therefore requires controlling for ecological variation between patches, which might be best achieved through experiments.

In forest ecosystems, management for timber production drastically alters the structure of forests and the availability of habitats therein (Müller et al., 2007). Forest management reduces quantity and quality of dead wood (Grove, 2002; Martikainen et al., 2000; Siitonen, 2001). Saproxylic species, which depend on dead wood, are among the most sensitive species groups affected by forestry (Brunet et al., 2010; Paillet et al., 2010), making them good indicators for entire forest biodiversity (Lachat et al., 2012; Stokland et al., 2012). Fresh dead wood represents a new habitat patch to be colonized by species over time. An enhanced amount of dead wood increases species richness, making it a critical key habitat for forest biodiversity (e.g. Bouget et al., 2012; Müller & Bütler, 2010). Seibold et al. (2017) further showed that local dead wood amount and dead wood in the surrounding landscape have independent positive effects on species richness. Yet, the mechanisms behind this increase in species richness go beyond the higher habitat and the thus increased resource availability. An increase in dead wood amount often leads to an increase in habitat heterogeneity and to better connectivity (Brin et al., 2009; Seibold et al., 2016). Conservation goals in (sustainable) forest management should thus require the enhancement of dead wood quantities and an optimized distribution across the landscape (Imesch et al., 2015; MCPFE, 2003). While dispersal ability might not be a limiting factor for many saproxylic species (Komonen & Müller, 2018), an even distribution to enhance connectivity of dead wood in the landscape can nevertheless be beneficial (Haeler et al., 2021).

Species communities in a habitat patch are influenced not only by habitat availability but also by environmental factors. Saproxylic species are known to be influenced by factors, such as temperature, light availability or moisture (Lachat et al., 2012; Siitonen et al., 2005; Sverdrup-Thygeson & Ims, 2002) and factors characterizing the dead wood pieces, such as tree species, decay stage and diameter (e.g. Grove, 2002; Stokland et al., 2012). By controlling for certain variables, experimental settings allow for the reduction in interfering heterogeneity, which leads to a better understanding of specific patterns. The manipulation of dead wood in experiments is a common method for studying saproxylic species, especially saproxylic beetles (see Seibold et al., 2015). Exposing dead wood to be colonized in an experimental setting and later reared in emergence traps allows for directly linking the species communities to the habitat patch, something that cannot be reached as accurately with other common trapping methods, such as flight interception

traps (Gossner, Floren, et al., 2013; Müller et al., 2015; Seibold et al., 2018). By controlling quantity and quality of dead wood pieces exposed, it is possible to gain insights at the object level and to study the drivers of colonizing species.

Our study aims at understanding how the distribution of dead wood in the landscape affects the colonization of new habitat patches by saproxylic beetles. We used an experimental approach, where we assembled different sized branch bundles from freshly cut branches (European beech, *Fagus sylvativa*) to represent otherwise homogeneous habitat patches. This allows us to focus on the effects of habitat patch size independent of habitat heterogeneity as a driving factor. The bundles were exposed for one season on forest plots situated along the two independent gradients of dead wood amount and isolation, describing dead wood availability in the surrounding landscape. Afterwards, branch bundles were reared in emergence traps. This experimental setting with standardized habitat patches allows us to answer the following questions:

1. Is species richness of saproxylic beetles higher or lower in a 'single large' branch bundle or in 'several small' accumulated bundles?
2. What are the effects of dead wood availability in the landscape and environmental factors on saproxylic beetles?
3. Does community composition differ between branch bundles of different sizes?

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The study was conducted in the Sihlwald forest reserve in Switzerland (47°15′20″ N, 8°33′00″ E), a 1100 ha large forest not managed for 20 years, dominated by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*; Brändli et al., 2020; Brang et al., 2011). The forest covers an elevation range of 467–915 m a.s.l. and is mainly northeast-exposed. To minimize heterogeneity besides variables describing dead wood availability in the landscape, we used a stratified random sampling to select 62 plots from a network of forest inventory plots in mature stands with at least 50% deciduous trees along two dead wood gradients: dead wood amount and isolation in a 40 m radius (for details on plot selection see Haeler et al., 2021).

To study the importance of the size of the habitat patch, we installed different sized bundles consisting of standardized branches to reduce heterogeneity on every plot. The branches were cut from freshly felled beech trees, and we made bundles of one, three, six and 12 branches (Figure 1). The branches had a diameter between three and six centimetres and a length of 80 cm. The exact diameter of the branches was measured to compute the total surface of each bundle (mean surface of branch bundles: one = 1494 ± 133 cm^2, three = 3417 ± 294 cm^2, six = 6511 ± 474 cm^2, twelve = 13,249 ± 721 cm^2, Figure 2).

On all plots we selected four trees, one in each cardinal direction from the plot centre (north, east, south and west) and randomly assigned one bundle of the four different sizes to each tree. We preferably selected beech trees with similar diameter at breast height but if none was available other deciduous trees were used. The bundles were fixed at a height of 130 cm facing south. Finally, the distance between the branch bundles was 23.6 ± 6.8 m on average ranging from 7.7 to 47.3 m in extreme cases, caused by the absence of fitting trees or inaccessible terrain. The bundles stayed in the forest from December 2016 to February 2018, that is, for the growing season 2017. The fieldwork and collection of beetles were granted by the Office for Landscape and Nature ('Amt für Landschaft und Natur', ALN) of the Canton Zurich (reference number: FNS 16248/tb/ht).

After retrieving the bundles from the forest, the branches were reared in ex situ emergence traps (Figure 1) for one season (2018). The emergence traps were PP tubes with a diameter of 20 cm. In the back, the tubes were closed with a thick black fabric. In the front, the tubes had a plastic lid with a collecting bottle, which contained 70% alcohol. The bundles were randomly assigned to the tubes, and the 12-branch bundle was split between two traps next to each other both containing six branches.

All species were identified and later assigned whether they are saproxylic based on an extended version of a list compiled by Schmidl and Bußler (2004). In addition to analysing the saproxylic beetles classified in this way (presented in the manuscript), we also repeated the analyses for all beetles as they still used the branch bundles as habitat (see Appendix S1 in the Supporting Information, Tables S4–S7 and Figures S9–S14).

2.2 | Dead wood in the landscape and environmental variables

To account for dead wood availability in the landscape, we calculated dead wood amount and isolation in concentric circles of 20–200 m (10 m steps) around each branch bundle based on a dead wood map created from LiDAR-data and complemented by digitizing lying dead wood from stereoscopic aerial imagery (Table S1). We calculated dead wood amount as the summed length of all mapped dead wood pieces within the each radius (20–200 m). Isolation was calculated as the median distance from the branch bundle to these dead wood pieces within the respective radius. For more details, see Haeler et al. (2021).

Additionally, we used temperature and light availability as environmental variables because they directly influence the characteristics of dead wood and thus the colonizing communities. As a temperature variable, we took high summer temperatures (mean from May, June and July) derived from hourly measurements at each plot with a HOBO Pendant® temperature data logger (UA-001-08; Onset Computer Corporation, Bourne, USA). Light availability for each branch bundle was calculated as the direct shortwave radiation (SWR) under maximum potential (i.e. cloud-free sky) from synthetic hemispherical images created from LiDAR data using the software Lidar2HemiEval (Webster et al., 2020).

FIGURE 1 Left + middle: The four different branch bundle sizes that were installed at each plot: one, three, six and 12 branches. Each bundle can be seen as one habitat patch. Right: Emergence traps consisting of closed PP tubes with an alcohol filled collecting bottle attached in the front.
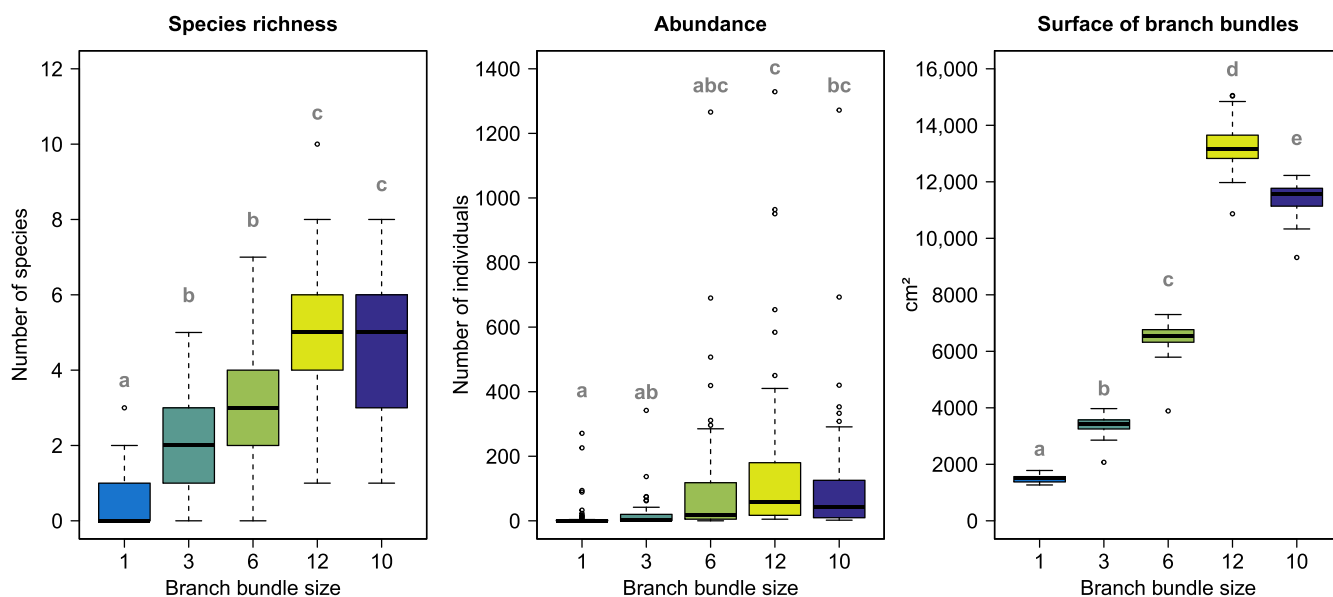

FIGURE 2 Left + middle: Boxplots for species richness and abundance (saproxylic species) for every branch bundle size (blue—one branch, dark green—three branches, light green—six branches and yellow—12 branches). Dark violet boxplots represent numbers for the pooled bundle with 10 branches (1 + 3 + 6 branches). The abundance plot was cut off at 1400 and is not showing one value with 2982 individuals (12 branches). Right: Boxplots for total surface (in cm^2) for every branch bundle size. Significant differences between groups were tested with an ANOVA and a post hoc Tukey's test (indicated by letters).

2.3 | Single Large Or Several Small

For the comparison between species richness and abundance in several small bundles compared with one large bundle (12 branches), we combined the small bundles (one, three and six branches) of each plot to a 'pooled bundle' consisting of 10 branches. We tested whether species richness and abundance differed between several small bundles pooled together compared with one large bundle using an ANOVA and a post hoc Tukey's test.

Furthermore, we calculated cumulative species–area curves (Quinn & Harrison, 1988) once by adding branch bundles from the smallest to the largest (based on the surface of the bundles) and once by adding them from largest to smallest. This shows whether a certain accumulated surface harbours more species when composed of a few large bundles or of a higher number of smaller bundles.

2.4 | Effects of dead wood in the landscape and environmental factors

For investigating the drivers of species richness and abundance in the branch bundles, we used generalized linear mixed models (GLMMs) with a Poisson distribution for species richness and a negative binomial distribution for abundance (function *glmmTMB* from the package 'glmmTMB', Brooks et al., 2022). We used plot number as a random effect to account for heterogeneity besides our focal explaining variables, which comprised the following: total surface of branch bundle (log-transformed), dead wood amount and isolation (in 20–200 m, 10 m steps), summer temperature and light availability. The models were calculated separately for each radius from 20 to 200 m in 10 m steps with the respective values for dead wood amount and isolation. See Appendix S1 (Table S1, Figures S1–S5) for details on the variables, models and residual analyses, which were performed with the package 'DHARMa' (Hartig, 2019). All statistical analyses were performed using R Version 4.1.1 (R Core Team, 2021). In the manuscript, we present the results for the 40 m radius with which the plot selection was done, results from all scales are reported in Appendix S1 (Tables S2 and S3).

2.5 | Analysis of community composition

To assess whether community composition differed between branch bundles of different sizes, we used a principal coordinate analysis (PCoA) as an unconstrained ordination (function *pcoa*, package 'ape'; Paradis et al., 2019). We calculated the Soerensen Index, which is based on presence–absence data, and the Bray–Curtis Index, which includes abundance data (*beta.pair* and *beta.pair.abund*, package 'betapart'; Baselga et al., 2017) to use with the PCoA. We further tested with distance-based redundancy analysis (dbRDA) (function *capscale*, package 'vegan'; Oksanen et al., 2018) if differences in community composition are related to the surface of the branch bundle, dead wood amount and isolation (in a 40 m radius), temperature and light availability.

3 | RESULTS

In total, we found 66 beetle species (23,511 individuals) of which 43 were classified as saproxylic (20,873 individuals). This represents a small proportion of the overall species pool from the study site, as we found 775 species (327 saproxylic species) with flight interception traps on the same plots (Haeler et al., 2021). The analyses for saproxylic species and all species yielded qualitatively similar results and we present the results considering saproxylic species here (see Appendix S1 for all species).

3.1 | Single large or several Small

Species richness and abundance of saproxylic beetles generally increased with branch bundle size, and we found 16 (one branch), 20 (three branches), 28 (six branches) and 33 (12 branches) species. The pooled bundles of 10 branches (1 + 3 + 6 branches) showed the same total species richness (33 species) and a similar mean (mean = 4.7 ± 1.9) as the large bundle of 12 branches (mean = 5.3 ± 1.6), despite having a significantly lower total surface (Figure 2). Ten branches had a mean surface of 11,419 ± 545 cm^2 compared with 12 branches with a mean surface of 13,249 ± 721 cm^2.

The comparison of the cumulative species–area curves adding the species from the smallest to the largest bundle and vice versa shows no continuous pattern between the curves (Figure 3). However, up until one-third of the cumulated surface the small-to-large curve
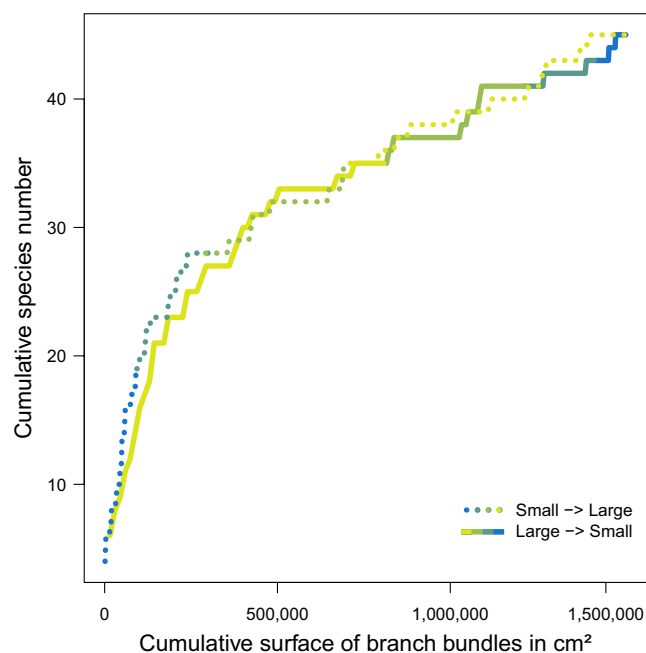

FIGURE 3 Cumulative number of saproxylic beetle species increases with cumulative surface of branch bundles. Change along *x*-axis: dotted line (blue to yellow)—adding branch bundles from small to large, solid line (yellow to blue)—adding branch bundles from large to small. Blue—one branch, dark green—three branches, light green—six branches, yellow—12 branches.

(blue to yellow) is above the large-to-small curve (yellow to blue). Also the species accumulation curves for each branch bundle size show that bundles with one and three branches have a fast increase in species numbers, but they are expected to reach a plateau relatively soon (Figures S7 and S8, left). While the species accumulation curve of the pooled bundle is only slightly above that of the bundle with 12 branches, it reaches a similar total species number with less branch surface (Figures S7 and S8, right).

3.2 | Effects of dead wood in the landscape and environmental factors

Beside bundle surface as the main driver of species richness and abundance of saproxylic beetles, dead wood availability in the surroundings played a minor role (Table 1, Tables S2 and S3). On scales up to 200 m, we found no relationship with dead wood amount, but isolation showed a negative relationship with abundance on several larger spatial scales (Table S3). Abundance was further positively related to temperature and species richness to light availability.

3.3 | Community composition

Species communities of the smaller bundles (one and three branches) were not completely nested in those of larger bundles (six and 12 branches). The large branch bundles with 12 branches had the highest number of unique species (10 species) compared with the other branch bundle sizes, which had two (one branch), two (three branches) and four (six branches) unique species (Venn diagram Figure S6). When combining the smaller branch bundles to the pooled bundle, 10 unique species were found, which did not occur in the large bundle. The principal coordinate analysis (PCoA) based on the Soerensen Index (presence–absence) revealed differences in community composition between the different branch bundle sizes (Figure 4, left). Branch bundles with one and three branches differed in their community composition compared with six and 12 branches,

which did not differ from each other. This separation between one and three compared with six and 12 branches was highlighted by the PCoA based on Bray–Curtis dissimilarities, which includes abundance data (Figure 4, right).

The *capscale* analysis revealed that differences in community composition were related to the surface of the branch bundles, but not to dead wood availability in the surroundings (Table 2). Differences in community composition were further related to temperature in analyses considering both presence–absence and abundances.

4 | DISCUSSION

Using a landscape experiment, we manipulated the size of habitat patches for saproxylic beetles by exposing branch bundles for 1 year in the forest. By pooling the beetles sampled from the three small bundles, we found the same species numbers compared with the largest bundle, even though the total bundle surface was smaller. This indicates that compared with a 'single large' habitat patch, 'several small' ones have the potential to harbour a higher diversity (SLOSS debate, e.g. Diamond, 1975; Fahrig, 2020; Fahrig et al., 2022). Due to the standardization of the habitat patches in this study (i.e. the exposed dead wood), this suggests an important role of microsite heterogeneity introduced through their distribution in the landscape. While dead wood in the SLOSS debate can be assessed on larger spatial scales (Mason & Zapponi, 2016; Sverdrup-Thygeson et al., 2014) to address the distribution of forest reserves with higher dead wood amounts (Bouget & Parmain, 2016), their establishment might not be feasible in all cases. The retention of dead wood in managed forest, on the contrary, is a measure that can easily be implemented by forest owners/managers. In the context of (sustainable) forest management, our findings can thus help design conservation measures on how dead wood should best be distributed in the forest.

Concentrating on the distribution within the forest, our results show that the same dead wood surface consisting of many small bundles rather than few large bundles can harbour more species (Figure 2).

TABLE 1 Results table of the glmer for species richness (left) and abundance (right) of saproxylic beetles. A grey background indicates variables with a *p*-value <0.05. Results for all scales are shown in Tables S2 and S3, results for all species are shown in Tables S4–S6.

Variable	Species richness (Poisson)				Abundance (negative binomial)			
	Estimate	SE	z-value	p-value	Estimate	SE	z-value	p-value
Conditional model								
Log10(Surface of branch bundle)	1.981	0.131	15.134	<0.001	3.043	0.374	8.138	<0.001
Dead wood amount (40 m radius)	−0.598	0.540	−1.107	0.268	−1.931	1.513	−1.276	0.202
Isolation (40 m radius)	0.072	0.040	1.790	0.074	0.099	0.126	0.784	0.433
Temperature	−0.030	0.041	−0.723	0.470	0.335	0.168	1.989	0.047
Light availability	0.092	0.040	2.291	0.022	0.224	0.161	1.392	0.164
Log10(Surface of branch bundle) * Dead wood amount	0.161	0.139	1.154	0.248	0.558	0.390	1.431	0.153
Dispersion model								
Log10(Surface of branch bundle)	(fixed dispersion parameter)				1.957	0.364	5.372	<0.001

Presence–absence (Soerensen)
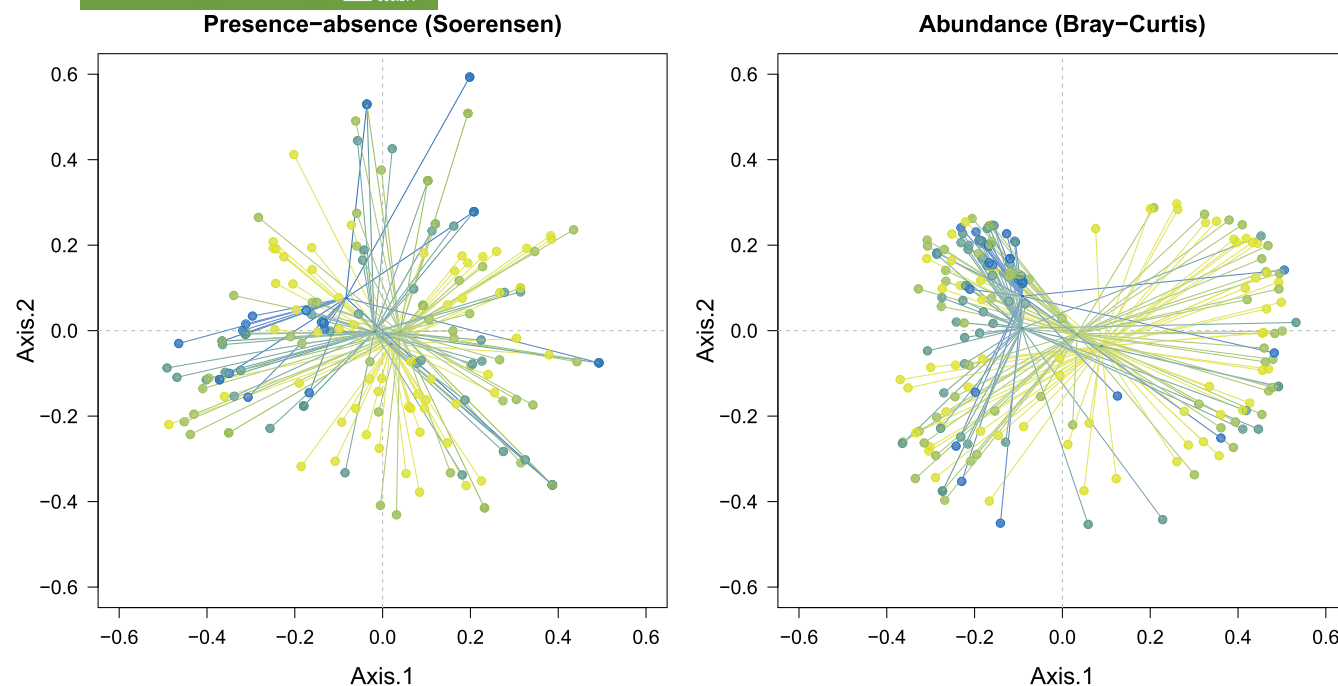
Abundance (Bray–Curtis)

FIGURE 4 Results of PCoA for saproxylic beetle species. Left: presence–absence data (Soerensen). Right: abundance-data (Bray–Curtis). Every point represents one branch bundle (blue—one branch, dark green—three branches, light green—six branches and yellow—12 branches). The lines connect every bundle with the centroid of the respective branch bundle size.

Variable	Presence-absence (Soerensen)		Abundance (Bray–Curtis)	
	F-value	*p*-value	*F*-value	*p*-value
Surface of branch bundle	6.669	0.001	5.393	0.001
Dead wood amount (40 m radius)	0.812	0.633	0.983	0.461
Isolation in (40 m radius)	0.798	0.668	0.811	0.680
Temperature	3.572	0.001	2.793	0.004
Light availability	1.243	0.242	0.870	0.595

TABLE 2 Results from the *capscale* analyses showing the relationship between community composition of saproxylic beetles and explaining variables. A grey background indicates significance $p < 0.05$.

Yet, this effect might diminish after a certain amount is reached (Figure 3). More saproxylic beetle species in combined smaller dead wood patches were explained by Seibold et al. (2016, 2017) through dead wood diversity regarding size and tree species, as habitat diversity and species diversity are strongly correlated (Hutchinson, 1959; Rosenzweig & Abramsky, 1993; Tews et al., 2004). Our experiment was designed to focus on the quantity of habitat by minimizing its heterogeneity, which was achieved by creating the different sized bundles from single standardized fresh cut branches. Still, we observed higher dissimilarities in community composition between small bundles compared with large ones (Figure 4), which could be explained by different environmental conditions across several smaller patches promoting habitat heterogeneity and consequently leading to more species (Fahrig, 2020; Rösch et al., 2015).

Microsite-heterogeneity is generally difficult to evaluate, but our results suggest it could play a key role in providing appropriate ecological conditions to different species. Especially, as small differences in the environment (e.g. sun exposure or wind conditions)

can lead to variable conditions between dead wood pieces (Seibold et al., 2016; Stokland et al., 2012; Vogel et al., 2020) and even within a single piece (Lettenmaier et al., 2022). In our results, this is partly reflected in the relationship between light availability and species richness and the relationships between temperature and abundance as well as community composition. The three smaller bundles further experienced a wider range of environmental conditions as they were spatially distributed (even though they were on average only 20 m apart), which was not the case for the large bundle. Additionally, spatially distributed bundles might have a higher chance to be initially found by a wider range of species, which could stimulate two processes affecting their colonization history. On one hand, colonized branch bundles might get unattractive for several other species due to competition for the resource and possibly caused by emitted pheromones (Brin & Bouget, 2018; Wende et al., 2017). On the other hand, initial species 'prepare the way' for associated beetles species, or species that depend on certain wood-decaying fungi, transmitted by the first colonizers (Heilmann-Clausen & Christensen, 2004;

Seibold et al., 2019). Populations in smaller habitat patches are also more susceptible to ecological drift (Gilbert & Levine, 2017; Riva & Fahrig, 2023). The importance of microsite-heterogeneity and colonization history hence increases over time as differences of the microhabitats get more pronounced during the development of the dead wood resulting in diverse species communities.

Compared with the impact of the size and the distribution of the branch bundles, the availability of dead wood in the surroundings up to 200m played a minor role. We never found a relationship with dead wood amount, but on some larger scales, a negative relationship between abundance and isolation was observed. That this did not reflect on species richness might be explained by the fact that the majority of saproxylic beetles are perceived as good dispersers (Janssen et al., 2016; Komonen & Müller, 2018; Ranius, 2006). Especially, dead wood is a dynamic habitat scattered across the landscape and saproxylic species constantly have to look for new suitable habitat that meets their ecological requirements (Jonsson et al., 2005). Furthermore, the first decay stages last shorter than later stages as the chemistry in the decaying wood changes quickly at the beginning (Stokland et al., 2012), leading to a high mobility of early colonizers. The results of the forest inventory show that the largest share of the overall volume of dead wood can be found in early decay stages. This is not surprising as the Sihlwald was managed intensively until a few decades ago. Still, the higher variability regarding tree species and decay stages (i.e. partly different habitats compared with the fresh branches used in this experiment) is not fully included in the variables calculated from the dead wood map. This, and that mainly the mobile early colonizers were attracted by the branch bundles, possibly explains the missing relationship of species richness with dead wood in the landscape. For species with lower dispersal abilities than early colonizers (e.g., certain red-list-species) habitat availability in the direct surroundings might be of higher importance (Brunet & Isacsson, 2009; Ranius & Fahrig, 2006).

5 | CONCLUSIONS

Our study, which based on data from a semi-controlled landscape experiment, demonstrates that a higher dead wood surface leads to an increase of species richness. However, in forest management, where enhancing dead wood availability is desirable, the question remains: When a certain amount of dead wood is available, how should it best be distributed in the landscape? The heterogeneity of (developing) habitats and species communities appears to be higher in several distributed small patches than in a single large patch, even if the 'starting point' was dead wood of the same dimensions and same tree species. It is important to emphasize that we did not compare several dead wood pieces with a small diameter to one piece with a large diameter, which can harbour very different species communities and cannot be replaced by cumulated dead wood of small diameters (Brin & Bouget, 2011; Grove, 2002; Heilmann-Clausen & Christensen, 2004). Large dead wood is an important habitat for saproxylic communities, but hardly available in managed forests (Gossner, Lachat, et al., 2013; Grove, 2002; Siitonen et al., 2000) and heterogeneity should be

increased by providing dead wood of all diameter classes. Yet, dead wood remaining after logging activities is often quite homogeneous regarding both species and diameter. Ensuring that these logging residues are spread over the landscape in different-sized and -composed patches and are not kept in one place increases habitat heterogeneity. This is probably caused by small differences in environmental conditions (e.g. sun exposure, temperature) and/or various colonization histories, supporting the development of a more diverse species community. A spread out distribution of dead wood further leads to a higher habitat connectivity, which had been shown to be important for different saproxylic species groups (e.g. Haeler et al., 2021). Nevertheless, the spatial distribution cannot make up for low dead wood amounts and should mainly be considered as an additional supporting measure alongside dead wood enrichment.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interests to declare.

DATA AVAILABILITY STATEMENT

Data available via EnviDat https://www.doi.org/10.16904/envidat.455 (Haeler et al., 2023).

ORCID

Elena Haeler https://orcid.org/0000-0002-3732-4565
Jonas Stillhard https://orcid.org/0000-0001-8850-4817
Loïc Pellissier https://orcid.org/0000-0002-2289-8259
Thibault Lachat https://orcid.org/0000-0003-3952-7443

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SUPPORTING INFORMATION

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

Figure S1. Residual plots for species richness-model (saproxylic species) from the *plot.DHARMa()* function. Left: QQ-plot to detect overall deviations from the expected distribution. Right: plot of the residuals against the predicted value.

Figure S2. Result from function *testDispersion*() comparing the dispersion of simulated residuals to observed residuals.

Figure S3. Residual plots for abundance-model (saproxylic species) from the *plot.DHARMa()* function. Left: QQ-plot to detect overall deviations from the expected distribution. Right: plot of the residuals against the predicted value.

Figure S4. Residual plots for species richness-model (all species) from the *plot.DHARMa()* function. Left: QQ-plot to detect overall deviations from the expected distribution. Right: plot of the residuals against the predicted value.

Figure S5. Residual plots for abundance-model (all species) from the *plot.DHARMa()* function. Left: QQ-plot to detect overall deviations from the expected distribution. Right: plot of the residuals against the predicted value.

Figure S6. Venn diagram of branch bundle sizes, showing numbers of shared and exclusive species (saproxylic species).

Figure S7. Species accumulation curves for saproxylic species (solid lines) along the cumulated dead wood surface of the bundles for each branch bundle size. Left: blue=1 branch, dark green=3 branches, light green=6 branches, yellow=12 branches. Right: dark violet=10 branches (pooled bundle), yellow=12 branches. Points represent the actually found species number of each bundle size. Dashed lines show predictions from function *iNext* how the species numbers could develop by adding more branches/surface.

Figure S8. Same accumulation curves as Figure S7 but including confidence intervals (95%) from the predictions calculated with the function *iNext*. Species accumulation curves for saproxylic species (solid lines) along the cumulated dead wood surface of the bundles for each branch bundle size. Left: blue=1 branch, dark green=3 branches, light green=6 branches, yellow=12 branches. Right: dark violet=10 branches (pooled bundle), yellow=12 branches. Points represent the actually found species number of each bundle size. Dashed lines show predictions from function *iNext* how the species numbers could develop by adding more branches/surface.

Figure S9. Left + middle: Boxplots for species richness and abundance (all species) for every branch bundle size (blue=one branch, dark green=three branches, light green=six branches and yellow=twelve branches). Dark violet boxplots represent numbers for the pooled bundle with ten branches (1+3+6 branches). The abundance plot was cut off at 1400 and is not showing one value with 2987 individuals (twelve branches). Right: Boxplots for total surface (in cm^2) for every branch bundle size. Significant differences between groups were tested with an ANOVA and a post-hoc Tukey-test (indicated by letters).

Figure S10. Cumulative number of all beetle species increases with cumulative surface. Change along *x*-axis: dotted line (blue to yellow)=adding branch bundles from small to large, solid line (yellow to blue)=adding branch bundles from large to small. Blue=one branch, dark green=three branches, light green=six branches, yellow=twelve branches.

Figure S11. Venn diagram of branch bundle sizes, showing numbers of shared and exclusive species (all species).

Figure S12. Results of PCoA for all beetle species. Left: presence-absence data (Soerensen). Right: abundance-data (Bray–Curtis). Every point represents one branch bundle (blue=one branch, dark green=three branches, light green=six branches and yellow=twelve branches). The lines connect every bundle with the centroid of the respective branch bundle size.

Figure S13. Species accumulation curves for all species (solid lines) along the cumulated dead wood surface of the bundles for each branch bundle size. Left: blue=1 branch, dark green=3 branches, light green=6 branches, yellow=12 branches. Right: dark violet=10 branches (pooled bundle), yellow=12 branches. Points represent the actually found species number of each bundle size. Dashed lines show predictions from function *iNext* how the species numbers could develop by adding more branches/surface.

Figure S14. Same accumulation curves as Figure S13 but including confidence intervals (95%) from the predictions calculated with the function *iNext*. Species accumulation curves for all species (solid lines) along the cumulated dead wood surface of the bundles for each branch bundle size Left: blue=1 branch, dark green=3 branches, light green=6 branches, yellow=12 branches. Right: dark violet=10 branches (pooled bundle), yellow=12 branches. Points represent the actually found species number of each bundle size.

Dashed lines show predictions from function *iNext* how the species numbers could develop by adding more branches/surface.

Table S1. Description of the variables used in the models.

Table S2. Result table for saproxylic species of the glmer for species richness on scales from 20 to 200 m. A grey background indicates variables with a *p*-value < 0.05. Results for all species are shown in Table S5.

Table S3. Result table for saproxylic species of the glmer for abundance on scales from 20 to 200 m. A grey background indicates variables with a *p*-value < 0.05. Results for all species are shown in Table S6.

Table S4. Result table for all species of the glmer for species richness (left) and abundance (right). A grey background indicates variables with a *p*-value < 0.05.

Table S5. Result table for all species of the glmer for species richness on scales from 20 to 200 m. A grey background indicates variables with a *p*-value < 0.05.

Table S6. Result table for all species of the glmer for abundance on scales from 20 to 200 m. A grey background indicates variables with a *p*-value < 0.05.

Table S7. Results from the *capscale* analyses showing the relationship between community composition and explaining variables for all beetles. A grey background indicates significance *p* < 0.05.

How to cite this article: Haeler, E., Stillhard, J., Hindenlang Clerc, K., Pellissier, L., & Lachat, T. (2024). Dead wood distributed in different-sized habitat patches enhances diversity of saproxylic beetles in a landscape experiment. *Journal of Applied Ecology, 61*, 316–327. https://doi.org/10.1111/1365-2664.14554