










RESEARCH ARTICLE

Drivers of community assembly change during succession in wood-decomposing beetle communities

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Funding information

Deutsche Forschungsgemeinschaft,
Grant/Award Number: Priority Program
1374 "Biodiversity Exploratories"

Handling Editor: Natalie Clay

Abstract

1. The patterns of successional change of decomposer communities is unique in that resource availability predictably decreases as decomposition proceeds. Saproxylic (i.e. deadwood-dependent) beetles are a highly diverse and functionally important decomposer group, and their community composition is affected by both deadwood characteristics and other environmental factors. Understanding how communities change with faunal succession through the decomposition process is important as this process influences terrestrial carbon dynamics.
2. Here, we evaluate how beta-diversity of saproxylic beetle communities change with succession, as well as the effects of different major drivers of beta-diversity, such as deadwood tree species, spatial distance between locations, climate and forest structure.
3. We studied spatial beta-diversity (i.e. dissimilarity of species composition between deadwood logs in the same year) of saproxylic beetle communities over 8 years of wood decomposition. Our study included 379 experimental deadwood logs comprising 13 different tree species in 30 forest stands in Germany. We hypothesized that the effects of tree species dissimilarity, measured by phylogenetic distance, and climate on beta-diversity decrease over time, while the effects of spatial distance between logs and forest structure increase.
4. Observed beta-diversity of saproxylic beetle communities increased over time, whereas standardized effects sizes (SES; based on null models) of beta-diversity

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decreased indicating higher beta-diversity than expected during early years. Beta-diversity increased with increasing phylogenetic distance between tree species and spatial distance among regions, and to a lesser extent with spatial distance within regions and differences in climate and forest structure. Whereas effects of space, climate and forest structure were constant over time, the effect of phylogenetic distance decreased.

5. Our results show that the strength of the different drivers of saproxylic beetle community beta-diversity changes along deadwood succession. Beta-diversity of early decay communities was strongly associated with differences among tree species. Although this effect decreased over time, beta-diversity remained high throughout succession. Possible explanations for this pattern include differences in decomposition rates and fungal communities between logs or the priority effect of early successional communities. Our results suggest that saproxylic beetle diversity can be enhanced by promoting forests with diverse tree communities and structures.

KEYWORDS

beta diversity, deadwood, decomposition, forest management, insect, saproxylic, succession

1 | INTRODUCTION

Understanding the mechanisms determining the temporal order of species' appearance in communities and the drivers of succession is among the oldest and most important questions in ecology (Clements, 1916; Fukami, 2015; Meiners et al., 2015; Odum & Odum, 1953). Succession of decomposer communities within a localized and stochastically ephemeral substrate, such as deadwood or carrion (Benbow et al., 2019), has received less attention compared to succession of plants and herbivores (Lasky et al., 2014; Li et al., 2016; Maren et al., 2017; Meiners et al., 2015; Walker & Wardle, 2014), but is no less important for ecosystem functioning. Decomposer succession coincides with predictable decreases in resource availability and concentrations of secondary metabolites related to plant defence as decomposition proceeds (Benbow et al., 2019). On quickly decomposing substrates, such as carrion and faeces, the succession of microbial and animal communities appears to be a predictable process (Metcalf et al., 2016; Payne et al., 1968). For communities inhabiting slowly decomposing resources, such as deadwood, however, changes in drivers of community assembly during succession remain poorly understood due to the rarity of long-term experiments (Seibold, Bässler, et al., 2015; Ulyshen & Hanula, 2010). Thus, it is not clear if the faunal succession in slowly decomposing resources is as deterministic as in quickly decomposing substrates.

Deadwood is key habitat for biodiversity in forest ecosystems (Stokland et al., 2012; Ulyshen, 2018) and plays an important role in the global carbon cycle (Pan et al., 2011; Seibold et al., 2021). Depending on deadwood size, wood traits, climatic conditions and the decomposer community (Bradford et al., 2014; Seibold et al., 2021; Weedon et al., 2009), complete deadwood decomposition takes from several

months to decades (Harmon et al., 2020). Insects, particularly saproxylic (i.e. deadwood-dependent) beetles, comprise a large portion of biodiversity associated with deadwood and are important agents of wood decomposition (Ulyshen, 2018). Many saproxylic species are threatened today as a result of forest management focusing on timber production and causing changes in habitat characteristics, such as decreases in deadwood amounts (Grove, 2002; Seibold, Brandl, et al., 2015). To conserve biodiversity of saproxylic species and to maintain the ecosystem function they provide, a better understanding of the drivers of community assembly of saproxylic species is needed.

Similar to herbivorous species (Brändle & Brandl, 2001; Kennedy & Southwood, 1984; Strong et al., 1984), many saproxylic species have adapted to the chemical and physical characteristics of their host tree species (Moll et al., 2021; Purahong et al., 2018; Wende et al., 2017). Since closely related tree species usually have similar wood characteristics, specialization with regard to host trees is rarely found at the level of tree species, but more frequently at the level of tree genera or plant functional groups, such as conifers or broadleaved tree species (Stokland et al., 2012). Since the concentration of secondary metabolites related to plant defence is highest right after tree death and decreases over time, it has been suggested that the degree of host specialization decreases with ongoing succession for saproxylic insects (Jonsell et al., 1998; Stokland et al., 2012; Ulyshen & Hanula, 2010) and fungi (Hanski, 1989; Jonsell & Nordlander, 2004). This process should lead to biotic homogenization over time, exhibited by decreasing spatial beta-diversity, as measured by the dissimilarity in species composition between saproxylic communities of different tree species at any specific point in time (Ferro, 2018). The trait database for saproxylic beetles from Northern Europe supports this hypothesis since species

with a higher degree of specialization dominate during early stages of decay, while host tree generalists prefer more the later stages of decay (Stokland et al., 2012). An alternative hypothesis is that there are persistent differences in community composition during wood decay, in particular between communities found in wood of conifer and broadleaved tree species, due to the deep evolutionary split and strong chemical and physical differences between these clades (Stokland et al., 2012). Moreover, differences in decomposition rates between tree species (Kahl et al., 2017) could maintain differences in wood decomposition between tree species and thus maintain high beta-diversity even if secondary compounds dissipate.

Furthermore, saproxylic communities depend not only on wood characteristics associated with tree species but also on the composition of preceding (Fukami et al., 2010; Jacobsen et al., 2015; Lunde et al., 2022; Weslien et al., 2011) and co-occurring communities (Jonsell et al., 2005; Ovaskainen et al., 2010). Positive and negative associations with co-occurring species and priority effects of early- on late-successional species, for example linked to niche modification (Fukami, 2015), can maintain beta-diversity over time despite increasing similarity in wood characteristics. The only experimental study to date analysing similarity of animal communities in deadwood over time reported taxonomic convergence of communities (Zuo et al., 2020). Yet, since various invertebrate groups were included which are only facultative users of deadwood, such as Annelida, Diplopoda and Isopoda, occurring especially during late decay stages, it remains unclear whether community convergence was only due to a shift from obligate to facultative saproxylic taxa.

In addition to mechanisms acting at the deadwood-log scale, community assembly of saproxylic communities is affected by spatial processes and environmental conditions (Neff et al., 2022). The composition of saproxylic communities varies spatially with beta-diversity increasing with increasing spatial distance between deadwood logs both within (Bae et al., 2020; Müller et al., 2020) and among regions (Bae et al., 2020). Such spatial patterns presumably reflect dispersal limitation (Chase & Myers, 2011) and differences in environmental conditions, such as temperature and precipitation, causing differences in regional species pools (Baselga, 2008). At large spatial scales, climatic conditions affect taxonomic alpha- and beta-diversity as well as functional diversity of saproxylic communities (Baselga, 2008; Friess et al., 2019; Hagge et al., 2019). At smaller spatial scales, saproxylic communities can be strongly influenced by management-related changes in, for example, canopy cover, tree species composition and deadwood amount (Hagge et al., 2019; Seibold, Bässler, et al., 2015). For example, at the regional level (~20km), differences in canopy cover can have stronger effects on community composition of saproxylic beetles than host tree species and spatial distance between deadwood logs (Müller et al., 2020; Vogel et al., 2020). Characteristics of saproxylic beetle species associated with spatial processes (e.g. dispersal ability; Komonen & Müller, 2018), forest structure (Bouget et al., 2015; Gibb et al., 2006) and microclimatic preferences (Möller, 2009) likely change with succession. Late successional species, for example, tend to be less specialized with regard to microclimate (Möller, 2009) and

are presumably weaker dispersers than early successional species (Ulyshen & Hanula, 2010), thus responding to forest structure at small rather than regional spatial scales (Jonsell et al., 2019). The effect of climate on beta-diversity of saproxylic beetle communities should thus decrease, whereas the effect of spatial distance and forest management should increase with proceeding faunal succession.

To study drivers of community assembly along succession in slowly-decomposing resources, we used deadwood and saproxylic beetles as study system. We exposed 379 experimental deadwood logs comprising 13 different tree species in a total of 30 forest plots. Plots were replicated in three regions of Germany with a maximum distance of ~600km between regions and spanned a gradient of forest management in each region. We sampled saproxylic beetle communities developing in these logs using emergence traps over 8 years of succession (2010–2017). To evaluate how the effects of tree species differences (quantified as phylogenetic distance between tree species), spatial distance between deadwood logs (decomposed into a within-region and an among-region component), differences in climate and differences in forest structure associated with forest management change over time, we analysed temporal patterns in spatial taxonomic beta-diversity and used multiple regression on distance matrices (MRM). We applied a generalized diversity framework, which provides a measure of beta-diversity which is independent from alpha-diversity (Chao, Chiu, et al., 2014), and which evaluates the influence of species' relative abundances by comparing Hill numbers (Chao, Gotelli, et al., 2014). We also assessed whether observed patterns were divergent from ecological stochasticity (Mori et al., 2015) by comparing observations to a null expectation of beta-diversity. In particular, we tested the following hypotheses:

Hypothesis 1 Spatial beta-diversity of beetle communities decreases over time (due to biotic homogenization of resources in the process of deadwood decomposition).

Hypothesis 2 Spatial beta-diversity increases with increasing phylogenetic distance between tree species (since closely related tree species have similar wood characteristics), but this effect decreases with ongoing succession.

Hypothesis 3 Spatial beta-diversity increases with increasing spatial distance between deadwood logs within and among regions, with differences in climate and differences in forest structure and effects increase with ongoing succession for spatial distance and forest structure but decrease for climate.

2 | MATERIALS AND METHODS

2.1 | Study design

The experiment is part of the Biodiversity Exploratories Project (Fischer et al., 2010) comprising three regions in Germany which span gradients of climate and geology: the UNESCO Biosphere Reserve

Schorfheide-Chorin (SCH) in the glacial moraine low-lands in north-eastern Germany (52°47'25"–53°13'26"N/13°23'27"–14°08'53"E, 3–140ma.s.l.), the Hainich National Park and surrounding area (HAI) in central Germany characterized by hills of calcareous bedrock covered by loess (50°56'14"–51°22'43"N/10°10'24"–10°46'45"E, 285–550ma.s.l.) and the UNESCO Biosphere Reserve Schwäbische Alb (ALB) in the low calcareous mountain range in south-western Germany (48°20'28"–48°32'02"N/9°10'49"–09°35'54"E, 460–860ma.s.l.). Annual precipitation ranged between 500 and 1000mm and mean annual temperature between 6 and 8.5°C across the three regions. The naturally dominant tree species in all three regions is European beech *Fagus sylvatica*, but due to the history of forest management, conifers make up considerable proportions of the forest area today (SCH: 39% *Pinus sylvestris*; HAI: 12% *P. sylvestris* and *Picea abies*; ALB: 24% *P. abies*). In each region, nine plots were selected to cover a gradient in forest management intensity from unmanaged beech forest (3 plots; unmanaged for at least 20years), to even-aged managed beech forest (3 plots) and to even-aged managed conifer forest (3 plots). In HAI, three additional plots were selected in uneven-aged managed beech forests, totalling to 30 plots.

The Biodiversity Exploratory Long-term Deadwood Experiment ('BElongDead') was established in 2009 (Gossner et al., 2016; Wende et al., 2017). On each plot, deadwood logs (approximately 4 m long and with a mean diameter of 31 ± 5.9 cm (SD)) of 13 tree genera (henceforth 'tree species' for simplicity) were experimentally exposed. Tree species included *Acer* sp., *Betula pendula*, *Carpinus betulus*, *F. sylvatica*, *Fraxinus excelsior*, *Larix decidua*, *P. abies*, *P. sylvestris*, *Populus* sp., *Prunus avium*, *Pseudotsuga menziesii*, *Quercus* sp. and *Tilia* sp. All logs were cut in winter 2008/2009 in the state of Thuringia (Germany), transported to each plot and placed in random order beside each other with approximately 1 m between logs. Due to limited availability, 10 plots did not have a *P. avium* log, one log of *Acer* sp. and *L. decidua* each was missing in HAI, resulting in a total of 379 sampled logs.

2.2 | Beetle sampling

Beetles emerging from the logs were sampled by closed emergence traps (Gossner et al., 2016) from 2010 to 2017. Traps were installed in March and sampling vials were emptied monthly until the end of October. Traps were dismantled for the winter and moved approx. 35cm along the log axis every year. Insects were sorted to order and beetles were identified to species level by taxonomic specialists. Species were classified as saproxylic according to Schmidl and Bußler (2004). Permits for collecting insects were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg. No further ethical approval was required.

2.3 | Predictor variables

To characterize the evolutionary distance between deadwood tree species, we used the ultrametric phylogeny of tree species from

Kahl et al. (2017). A forest inventory (Schall et al., 2018) and a deadwood inventory (Kahl & Bauhus, 2014) was conducted on all plots covering an area of 100m × 100m between 2008 and 2011. Canopy cover was assessed by airborne LiDAR during leaf-on conditions (HAI: 2008; SCH, ALB: 2009) for a 20m circle around the area where deadwood logs were deployed considering all forest strata 2 m above ground (Gossner et al., 2016). Since no LiDAR data were available for later years and since forest structures did not change strongly over time (Schall et al., 2018), the same forest structure data were used to characterize differences between plots for all years. Mean annual temperature and precipitation for each plot was calculated based on data from weather stations located at each plot for the period January 2010 to December 2017 (Wöllauer et al., 2021).

2.4 | Beta-diversity measures

We used a statistical framework based on Hill numbers to quantify beta-diversity between communities of saproxylic beetles. Hill numbers (i.e. the effective number of species) can be used to quantify and decompose taxonomic diversity measures (Hill, 1973). A major advantage of Hill numbers is that they obey the replication principle (Chao, Gotelli, et al., 2014) and can thus be decomposed into independent components of alpha- and beta-diversity in the range of [0, 1] (Chao, Chiu, et al., 2014). Hill numbers differ among themselves by a parameter q that reflects their respective sensitivity to species relative occurrence probabilities. For Hill numbers, multiplicative beta-diversity can be transformed to four types of dissimilarity: Jaccard-type turnover, Sorensen-type turnover, Jaccard-type non-overlap and Sorensen-type non-overlap (Chao et al., 2019). Setting $q = 0$ yields the richness-based Sørensen index, weighting all species equally and thus giving more weight to the many rare species that occur in a dataset. Setting $q = 1$ yields the Horn index, which weights all occurrences equally, that is, according to species' incidence-based frequency; therefore, it is sensitive to common species. Setting $q = 2$ yields the frequency-based Morisita-Horn index, which is most sensitive to dominant species. Different parameters of q thus reflect patterns in beta-diversity with emphasis on rare, common and dominant species, respectively. We calculated pairwise dissimilarities for $q = \{0, 1, 2\}$ by means of the SPADER package (Chao et al., 2016) in R (R Core Team, 2020), for all sample-pairs.

We used a null model approach to compare the observed beta-diversity to the beta-diversity expected under ecological stochasticity. Therefore, we compared the observed value of beta-diversity to the mean beta-diversity value obtained from 100 comparisons between two randomly drawn communities. These simulated communities were created by using a non-sequential algorithm for count matrices, which kept matrix sums and row/column sums constant (Gotelli & Entsminger, 2003). The standardized effect size (SES) was afterwards obtained by subtracting the mean simulated beta-diversity from the observed beta-diversity and afterwards dividing by the standard deviation of the simulated values.

2.5 | Statistical analyses

Statistical analyses were conducted in R version 4.2.0 (R Core Team, 2020). To test whether spatial beta-diversity changed over time, we fitted separate linear mixed models (function *lmer* in package *LME4*; Bates et al., 2015) for observed and SES beta-diversity for $q = 0, 1$ and 2. In each model, respective beta-diversity comparisons between logs within the same year were used as response variable and year as continuous variable (1–8) as fixed effect. A categorical variable defining whether sample pairs originate from the same plot, the same region or from different regions was included as random effect to account for the nested design of the study. To account for potential further dependencies among data, we applied a null model approach similar to Burner et al. (2021) repeating the same model 99 times for each response variable for randomized data by reshuffling beta-diversity values while keeping the sampleID pairs constant. To assess whether beta-diversity changed over time significantly, we compared the effect sizes of year between the models for observed and randomized data.

To study how drivers of spatial beta-diversity changed over time, we conducted multiple regression on distance matrices (function *MRM* in package *ECODIST*; Goslee & Urban, 2007) for each beta-diversity measure separately for each year. MRM models included five explanatory dissimilarity matrices which were each standardized to range of 0–1: phylogenetic distance between host tree species, dissimilarity based on forest structures, dissimilarity in climate, and two dissimilarity matrices partitioning spatial distances between logs into a within-region and a between-region component (for details on the calculation of distance matrices, see below). We then extracted F-values from MRM models and used separate linear models (function *lm*) for each beta-diversity measure and predictor to test whether effects of the respective predictor changed over time by including the year as continuous explanatory variable (1–8).

The phylogenetic distance matrix was calculated as the patristic distance between tree genera using the function *cophenetic.phylo* in the package *APE* (Paradis & Schliep, 2019). Dissimilarity based on forest structure equally considered the basal area, proportion of basal area represented by conifers, number of tree species, deadwood volume and canopy cover. Note that we used the term 'forest structure' for simplicity although the share of conifers represents forest composition. Dissimilarity in climate was based on mean annual temperature and annual precipitation sum. Both, dissimilarity in forest structure and dissimilarity in climate, were calculated as Euclidean distance between logs using the function *vegdist* after standardizing each considered variable (mean = 0, SD = 1; function *decostand* in *VEGAN*; Oksanen et al., 2018).

Since plots were clustered in three regions, the fine-scale spatial structure within each region could be easily masked by the large-scale spatial structure among regions. We, thus, partitioned spatial distances into a within-region and an among-region component following Bae et al. (2020). Therefore, a geographical distance matrix between the logs was calculated and then truncated by the minimum distance between the three regions. All pairwise distances larger than the minimum distance among regions were

then set to four times of the minimum distance among regions (for a detailed explanation why to use the multiplicate 'four', see Borcard & Legendre, 2002). We then used principal coordinates of neighbour matrices (PCNM) and the function *dbmem* in the package *ADESPATIAL* (Dray et al., 2012) which applies a principle component analysis resulting in distance-based Moran's eigenvectors orthogonal to one another. Of these eigenvectors, only the positive eigenvalues represent the Euclidean components of the neighbourhood relationships. Positive eigenvalues were extracted and subject to an analysis of variance model (ANOVA) using the function *aov* with region as the independent variable. This allowed disentangling the eigenvalues that differed significantly between regions and those that did not differ significantly between regions representing the spatial structure within regions. Based on these two sets of eigenvalues, we calculated the among-region and within-region dissimilarity matrices as Euclidean distances using the function *dist*.

3 | RESULTS

Over 8 years of succession, we sampled 66,199 individuals of 481 species of saproxylic beetles. Of these, 158 species (14,545 individuals) were xylo-phloeophages, (those feeding on bark, sapwood or heartwood), 120 species (31,440 individuals) were mycetophages, (feeding on fungi living on deadwood), and 188 species (20,170 individuals) were zoophages (predatory species feeding on other saproxylic animals).

Observed spatial beta-diversity of saproxylic beetles increased over time for all values of q (Figure 1; Figure S1; Table S1). The linear coefficients of year from models for observed data were beyond the 95th percentile of coefficients of the null models indicating that the increase in beta-diversity over time was significant (Figure 1). In contrast, the standardized effect size (SES) of beta-diversity showed the opposite patterns with significant decreases over time (Figure 1; Table S1) indicating higher dissimilarity than expected in early years, but these effects appear to be mainly driven by the first 2 years (Figure S1).

Observed spatial beta-diversity increased with increasing phylogenetic distance among tree species and spatial distance among regions for all values of q and in all years (Figure 2 and Table S2). Dissimilarity with regard to forest structure (i.e. canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume), climate and spatial distance within regions significantly affected observed spatial beta-diversity for all values of q , but not in all years. The SES of spatial beta-diversity increased with increasing dissimilarity in forest structure and spatial distance among regions in most years indicating higher beta-diversity than expected when differences in forest structure and distances between regions were high (Figure 2 and Table S2). Phylogenetic distance between tree species and dissimilarity in climate had significant positive effects on SES of beta-diversity only in some years. Effects of climate were negative in some years indicating that beta-diversity diverged less from the null expectation or was even smaller than expected despite high differences in climate. Spatial distance within regions significantly affected SES of beta-diversity only in very few years.

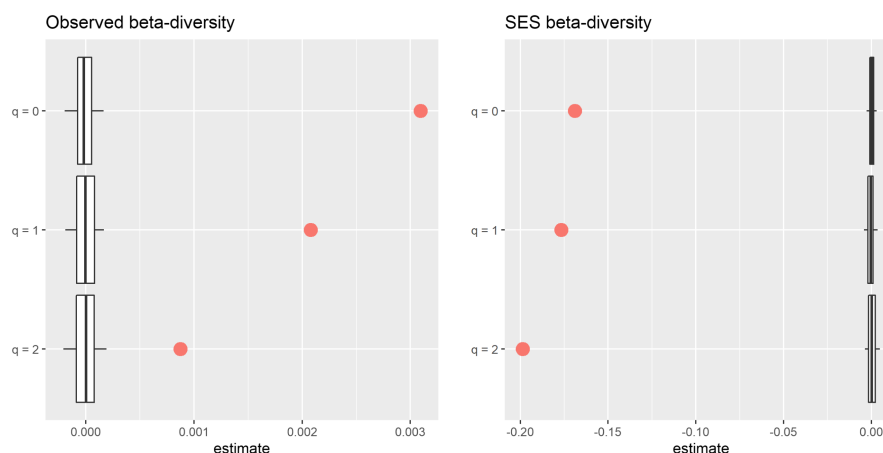


FIGURE 1 Linear coefficients of the effect of year on observed values (left) and standardized effect size (SES; right) of spatial beta-diversity of saproxylic beetles between logs within years along the series of Hill numbers ($q = 0$ – 2). Red circles indicate coefficients of models for observed data and boxplots show distribution of coefficients from 99 null models with randomized beta-diversity data. All observed coefficients are outside the 5th and 95th percentile and can thus be interpreted as significant. All models included a categorical variable describing whether sample pairs originate from the same plot, the same region or different regions to account for the nested design of the study.

The effect of phylogenetic distance decreased over time for observed spatial beta-diversity along the Hill series (Figure 2 and Table S3) and for SES of spatial beta-diversity except for $q = 0$ (Figure 3 and Table S3). The effects of dissimilarity in forest structure, climate and spatial distance within and among regions did not change significantly over time for observed beta-diversity (Figure 2 and Table S3). Similarly, the effects of dissimilarity in forest structure and spatial distance among regions on SES of beta-diversity did not change over time (Figure 3 and Table S3). In contrast, the effect of climatic dissimilarity between plots on SES of beta-diversity decreased over time and shifted from positive to negative indicating higher observed beta-diversity than expected when climatic differences were high during early years and lower beta-diversity than expected despite high climatic differences in later years. The effect of within-region spatial distance on SES of beta-diversity increased over time shifting from negative to positive. This indicates initially lower beta-diversity than expected despite high spatial distances within regions and higher beta-diversity than expected when spatial distances within regions were high in later years.

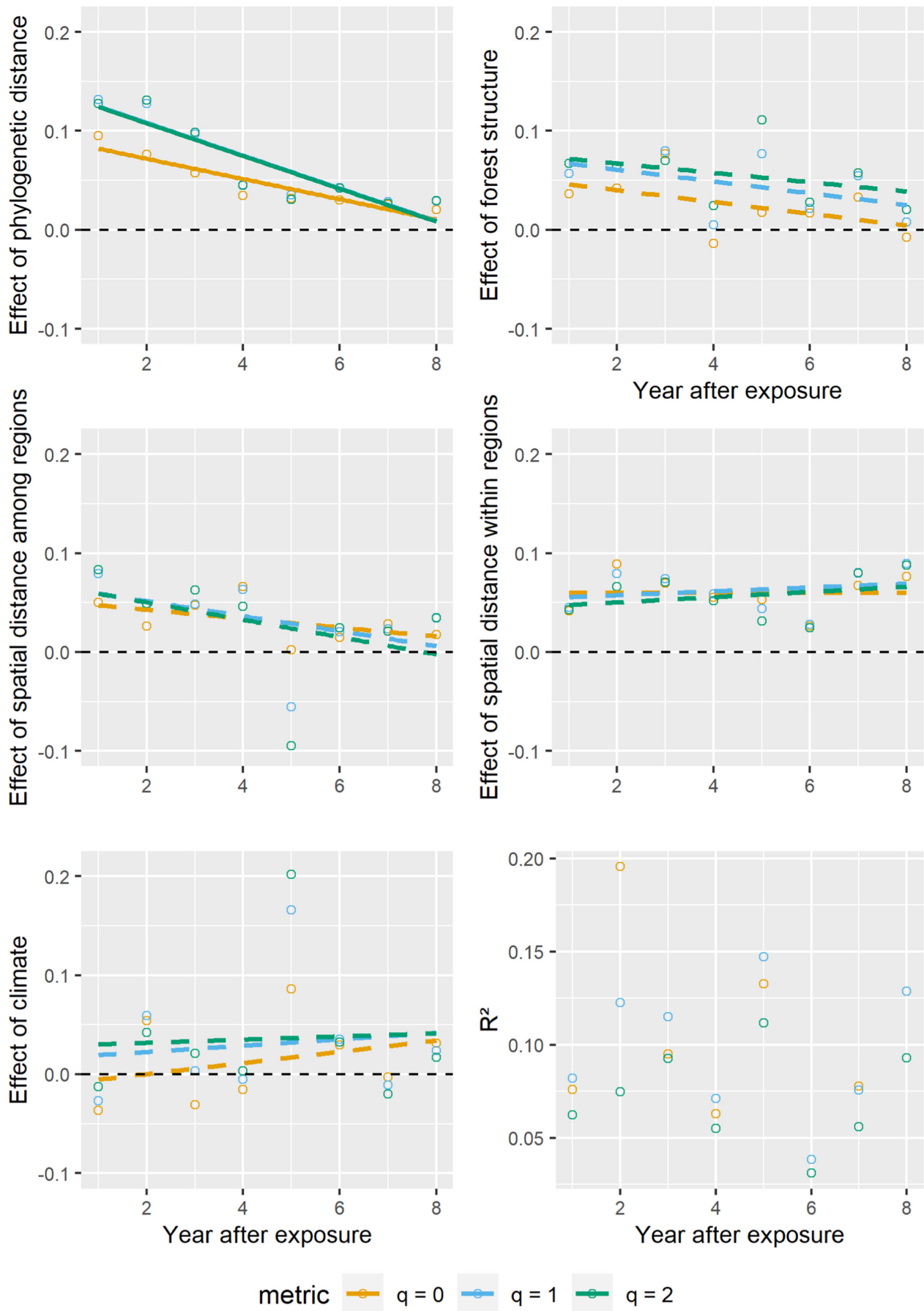
4 | DISCUSSION

Patterns of spatial beta-diversity over a time series of 8 years indicate that assembly patterns of saproxylic beetle communities change with faunal succession through the decomposition process.

Inconsistent with our first hypothesis, observed beta-diversity increased over time. Yet, the null-model approach showed that beta-diversity was higher than expected in early years but less so later on. Spatial beta-diversity was driven by phylogenetic distances between tree species, differences in forest structure and climate and spatial distances among regions. In line with our second hypothesis, the effect of phylogenetic distances between tree species on spatial beta-diversity decreased over time, but inconsistent with our third hypothesis, the influence of space, climate and forest structure remained constant over time for observed beta-diversity.

Trajectories of habitat conditions during succession differ fundamentally between decomposer communities and communities of plants and herbivores as decomposers face decreasing resource availability (Benbow et al., 2019). Changes in necromass characteristics are associated with distinct changes in decomposer communities (Benbow et al., 2019; Lee et al., 2014; Stokland et al., 2012; Ulyshen & Hanula, 2010; Zuo et al., 2020). Particularly in quickly decomposing necromass types, such as carrion, these changes appear to be strongly deterministic (Barton et al., 2013; Metcalf et al., 2016; Michaud et al., 2015). Yet, for slowly decomposing types of necromass, such as deadwood, community assembly may become increasingly stochastic over time as initial differences, for example tree-species specific differences in wood characteristics, gradually decrease during the decomposition process (Stokland et al., 2012; Ulyshen & Hanula, 2010). We thus hypothesized that spatial beta-diversity of saproxylic beetle communities decreases

FIGURE 2 Temporal change in the effect size of drivers of observed spatial beta-diversity between logs within years. Circles show F -values of MRM-analyses of observed beta-diversity values along the series of Hill numbers against three predictor dissimilarity matrices and the marginal R^2 . Predictor matrices were based on the phylogenetic distance between tree species, the differences in forest structure (i.e. canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume), spatial distances among and within regions and differences in climate (i.e. mean annual temperature and precipitation). Regression lines were derived from linear models (Table S3). Dashed lines indicate nonsignificant relationships ($p > 0.05$).



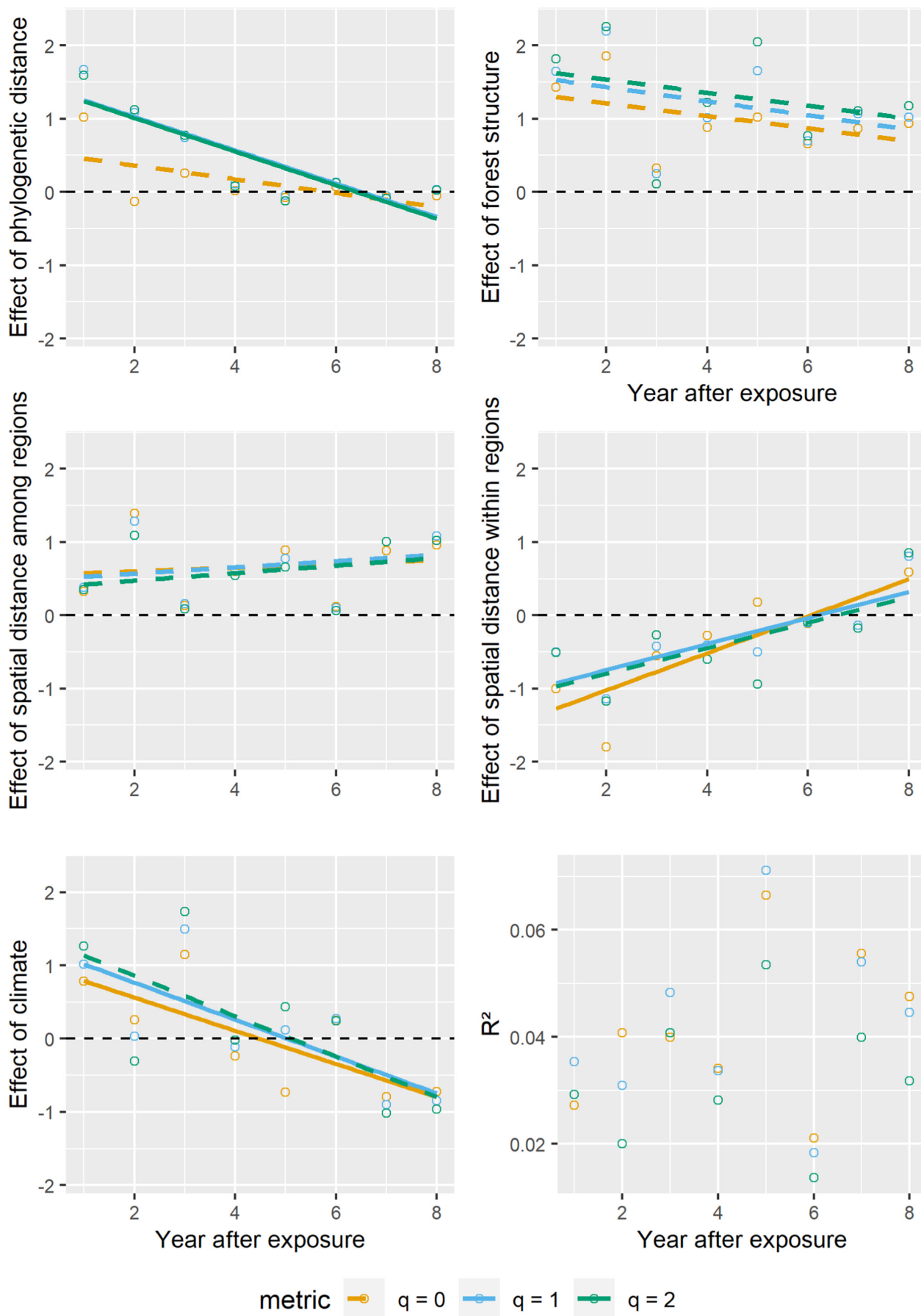


FIGURE 3 Temporal change in F -values indicating the effect size of drivers of standardized effect sizes (SES) of spatial beta-diversity between logs within years. Circles show F -values of MRM-analyses of SES beta diversity values along the series of Hill numbers against three predictor dissimilarity matrices and the marginal R^2 . Predictor matrices were based on the phylogenetic distance between tree species, the differences in forest structure (i.e. canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume), spatial distances among and within regions and differences in climate (i.e. mean annual temperature and precipitation). Regression lines were derived from linear models (Table S3). Dashed lines indicate nonsignificant relationships ($p > 0.05$).

over time. In contrast to our expectation, observed beta-diversity increased for all Hill numbers. The effect decreased from $q = 0$ to $q = 2$, indicating that rare species contribute more strongly to higher beta-diversity in later successional stages. This is similar to Thorn et al. (2020), demonstrating that rare species contributed most to community differences over time. Comparing observed beta-diversity to beta-diversity of null-model communities revealed higher beta-diversity than expected by chance for all Hill numbers, particularly in the first 2 years. Higher beta-diversity than expected by chance can be caused for instance by abundant species frequently occurring in randomly generated samples but in few observed samples with very high abundances. Early saproxylic beetle communities include rare, specialized species (in terms of habitat conditions), as well as some highly abundant species of which some show a high degree of host-tree specialization (Bussler et al., 2011), such as the bark beetle species (Scolytinae) *Crypturgus hispidulus*, *Crypturgus cinereus* and *Dryocoetes autographus* which were among the most abundant species during the first 2 years in our samples. Considering that observed beta-diversity increased more strongly over time for $q = 0$ and $q = 1$ than for $q = 2$, abundant but specialized species are likely the reason why beta-diversity was higher than expected by chance during early years of succession. This pattern suggests that the importance of stochasticity increases over time (Meiners et al., 2015; Pulsford et al., 2016) and supports the hypothesis that stochasticity becomes increasingly important for community assembly during decomposition of slowly decomposing necromass.

High values of observed spatial beta-diversity during later successional stages may be explained by several potential mechanisms. Decomposition rates vary among tree species but also among logs of the same tree species and even within single logs (Kahl et al., 2017; Saint-Germain et al., 2010). High habitat heterogeneity associated with differences in decay stages could be one driver of high spatial beta-diversity in later years (Müller et al., 2020). Moreover, saproxylic beetle communities in later successional stages of decay comprise many fungus-feeding species (Ulyshen & Hanula, 2010; Vanderwel et al., 2006). Studying saproxylic beetles in artificial high stumps 6 years after creation, Jonsell et al. (2005) found that the occurrence of two fungal species which differ in the rot type they produce was the main driver of beetle community composition. Since the share of fungus-feeding insects (Ulyshen & Hanula, 2010; Vanderwel et al., 2006), as well as fungal biomass and diversity increase over time (Boddy, 2001; Rajala et al., 2012), high spatial beta-diversity of saproxylic insects in later years could be associated with differences in fungal communities. Finally, early successional communities of beetles and fungi influence wood decomposition (Rajala et al., 2012;

Seibold et al., 2021; Ulyshen, 2016; Van Der Wal et al., 2015) and can thus affect the species composition of later-successional communities by reducing the amount of resources (niche preemption) and by modifying niches available to later-successional species, that is, via priority effects (Fukami, 2015). Priority effects have been documented for saproxylic communities in both laboratory experiments (Dickie et al., 2012; Fukami et al., 2010) and field experiments (Jacobsen et al., 2015; Weslien et al., 2011).

The *taxonomic-isolation hypothesis* predicts that herbivorous insects are more likely to switch to closely related hosts than to unrelated hosts since closely related hosts often share chemical and physical traits and thus, closely related tree species should have more similar herbivore communities than distantly related trees (Brändle & Brandl, 2001; Strong et al., 1984). Especially the phylogenetic split between gymnosperm and angiosperm species marks a clear divide in both herbivore (Leidinger et al., 2019, 2021; Sobek et al., 2009) and saproxylic insect communities (Bussler et al., 2011; Müller et al., 2020; Seibold et al., 2016; Vogel et al., 2021), but differences in community composition occur within both clades (Leidinger et al., 2021; Vogel et al., 2021). We thus hypothesized that beta-diversity increases with increasing phylogenetic distance between tree species. This hypothesis was supported by our results for observed and SES of beta-diversity. Furthermore, we hypothesized that the effect of phylogenetic distance between tree species on beta-diversity decreases over time since differences between tree species in wood traits, such as secondary compounds, are stronger during early stages of decay and gradually decrease during the decomposition process (Stokland et al., 2012; Wende et al., 2017). Our results confirmed this hypothesis; strong positive effects of phylogenetic distance between tree species occurred only during the first three study years. Effects of phylogenetic distances tended to be stronger for abundant and dominant species in early years, which may be explained by the occurrence of some abundant species with strong host tree preferences for single tree species or few closely related tree species during early successional stages (Bussler et al., 2011). This supports the hypothesis that tree-species specific differences in wood characteristics become less important as wood decays (Zuo et al., 2020). To identify wood traits that contribute most to differences in saproxylic communities, future research should link saproxylic community data to wood traits measured for the same logs and along a decay gradient.

Forest structure and composition, such as canopy cover, tree species composition and deadwood amount, determine habitat availability and quality and are thus important drivers of plant, fungal and animal communities, including saproxylic beetles (Janssen

et al., 2017; Lassauce et al., 2011; Leidinger et al., 2020; Penone et al., 2019). Our results show that beta-diversity of saproxylic beetle communities can be partially explained by forest structure and slightly more strongly for abundant and dominant species than rare species. Effects of forest structure did not change significantly over time in our study indicating that the forest environment is important for saproxylic beetle communities throughout succession. Since we assessed only the combined effect of canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume, further studies are needed to disentangle the relative importance of different forest structural and compositional characteristics for community assembly of saproxylic beetles.

Climatic differences are generally important drivers of diversity and community composition (Turner, 2004; Willig et al., 2003). At the European level including temperate and boreal countries, climatic variables explained beta-diversity of longhorn beetles (Cerambycidae) partly (Baselga, 2008), whereas no significant effects could be found for beta-diversity of saproxylic beetles inhabiting fruitbodies of the fungus *Fomes fomentarius* across temperate European beech forests (Friess et al., 2019). Our results suggest that climatic differences between plots were of minor importance for beta-diversity of saproxylic beetles since significant effects were found only in some years. Yet, for SES of beta-diversity the effect of climate changed over time significantly from positive to negative. This pattern suggests that high climatic differences caused higher observed beta-diversity than expected during early years, but lower observed beta-diversity than expected in later years. Even if the effect of climate on observed beta-diversity did not change over time, our results found for SES of beta-diversity support the hypothesis that climatic conditions are more important for saproxylic beetles during early than late stages of faunal succession. Here, we considered only climatic differences between plots based on mean temperature and precipitation across all study years. Further research is needed to evaluate effects of climate and weather at a more detailed scale considering not only longer-term averages but also seasonal aspects and anomalies (Welti et al., 2022).

Spatial distance between localities is a key driver of beta-diversity (Chase & Myers, 2011; Kraft et al., 2011). At large spatial scale, beta-diversity is considered to be associated with differences in regional species pools due to macro-scale environmental filtering, historical biogeography, and long-distance dispersal, whereas at small spatial scale, dispersal limitation, environmental filtering, and biotic interactions shape communities (Bae et al., 2020; Cadotte & Tucker, 2017; Chase & Myers, 2011). Decomposing spatial distances into an among-regions and a within-regions component, we found that observed and SES of spatial beta-diversity increased with increasing spatial distance at large spatial scale (among-regions) for all values of q and these effects were stable along the successional gradient. At the within-region scale, spatial distance was of minor importance for observed and SES of beta-diversity. However, within-region spatial distance had significant negative effects on SES of beta-diversity during early years indicating lower

beta-diversity than expected despite high spatial distances which may be due to the high dispersal ability of many early-successional species such as bark beetles (Hagge et al., 2021; Komonen & Müller, 2018). While Bae et al. (2020) reported that among-regional and within-region spatial structure had similar strong effects on saproxylic beetle communities, Müller et al. (2020) found only weak effects at the within-regional scale, similar to our results. Comparing the association of saproxylic beetle communities with habitat variables at small (<5 km) and larger spatial scales, Jonsell et al. (2019) reported stronger effects of small-scale variables on late- than on early-successional communities indicating that the importance of dispersal limitation may increase during succession. Overall, however, the proportion of studies reporting indications for dispersal limitation in saproxylic insects at small spatial scales is small (Komonen & Müller, 2018). Together, this suggests that processes related to larger spatial distance, such as macro-scale environmental differences, structure saproxylic beetle communities, whereas dispersal limitation at within-regional scales plays only a minor role which, however, tends to increase during succession.

5 | CONCLUSIONS

Based on data covering 8 years of succession in deadwood, our results indicate that drivers of community assembly of saproxylic beetles change over time. Early successional communities were determined by associations between tree and beetle species and thus spatial beta-diversity increased strongly with increasing phylogenetic distances between tree species. Although the effect of tree species on beta-diversity weakened over time, observed beta-diversity increased, rather than decreased, over time. Potential processes explaining this pattern include habitat heterogeneity linked to differences in decomposition rates, differences in fungal communities and priority effects of early successional beetle and fungal communities. Spatial beta-diversity was further affected by forest structure and spatial distance between deadwood logs at larger spatial scales (among regions) with their effects being stable over time. Within regions, we found no indication for dispersal limitation. Climatic conditions had overall weak effects but tended to be more important for early-successional communities. For conservation of saproxylic beetle diversity, our results suggest that biodiversity can be promoted by providing a high diversity of tree species and particularly by including distantly related tree species. Moreover, saproxylic beetle biodiversity benefits from variation in forest structure and thus structural heterogeneity should be promoted at the landscape scale. Finally, positive effects of spatial distance at large spatial scales on beta-diversity of saproxylic beetle communities indicate that conservation efforts should cover larger spatial extends to capture variation in environmental conditions.

AUTHOR CONTRIBUTIONS

Sebastian Seibold perceived the idea with inputs from Martin M. Gossner, Claus Bässler, Marc W. Cadotte and Akira S. Mori.

Sebastian Seibold, Wolfgang W. Weisser, Martin M. Gossner and Didem Ambarlı collected data. Sebastian Seibold and Simon Thorn analysed the data. Sebastian Seibold and Simon Thorn led writing with inputs of all co-authors.

ACKNOWLEDGEMENTS

We are grateful to Jasmin Bartetzko, Iris Gallenberger, Petra Freynhagen, Marco Lutz and Marina Schusser for field work and insect sorting, Alexander Szallies, Boris Büche, Frank Köhler, Heinz Bussler, Hans-Peter Reike, Torben Kölkebeck, Ludger Schmidt, Michael-Andreas Fritze and Thomas Wagner for species identification and Matthias Biber for cluster computing. We thank Christian Ammer, Peter Schall and Jürgen Bauhus for providing forest inventory data. We thank Claudia Seilwinder for maintaining the BELongDead Experiment and the managers of the three Exploratories, Swen Renner and Kirsten Reichel-Jung (Alb), Sonja Gockel, Kerstin Wiesner, Katrin Lorenzen and Juliane Vogt (Hainich) as well as Andreas Hemp, Martin Gorke, Miriam Teuscher (Schorfheide) and all former managers for their work in maintaining the plot and project infrastructure; Simone Pfeiffer, Maren Gleisberg, Christiane Fischer, Jule Mangels and Victoria Griebmeier for giving support through the central office, Andreas Ostrowski for managing the central data base, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank the administration of the Hainich National Park, the UNESCO Biosphere Reserve Schwäbische Alb and the UNESCO Biosphere Reserve Schorfheide-Chorin as well as all landowners for their collaboration. The work has been funded by the DFG Priority Program 1374 'BiodiversityExploratories'. Open Access funding enabled and organized by Projekt DEAL.







CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Biodiversity Exploratories Information System (<https://doi.org/10.17616/R32P9Q>; <https://www.bexis.uni-jena.de>) with dataset IDs 19007 for climate, 24546, 18270 and 30925 for forest structure (Schall et al., 2018) and 31123 for saproxylic beetles (Gossner et al., 2016).

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REFERENCES

- Bae, S., Heidrich, L., Levick, S. R., Gossner, M. M., Seibold, S., Weisser, W. W., Magdon, P., Serebryanyk, A., Bässler, C., Schäfer, D., Schulze, E. D., Doerfler, I., Müller, J., Jung, K., Heurich, M., Fischer, M., Roth, N., Schall, P., Boch, S., ... Müller, J. (2020). Dispersal ability, trophic position and body size mediate species turnover processes: Insights from a multi-taxa and multi-scale approach. *Diversity and Distributions*, 27, 1–15. <https://doi.org/10.1111/ddi.13204>
- Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., & Manning, A. D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, 171(4), 761–772. <https://doi.org/10.1007/s00442-012-2460-3>
- Baselga, A. (2008). Determinants of species richness, endemism and turnover in European longhorn beetles. *Ecography*, 31, 263–271. <https://doi.org/10.1111/j.2007.0906-7590.05335.x>
- Bates, D., Maechler, 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>
- Benbow, M. E., Barton, P. S., Ulyshen, M. D., Beasley, J. C., DeVault, T. L., Strickland, M. S., Tomberlin, J. K., Jordan, H. R., & Pechal, J. L. (2019). Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, 89(1), 1–26. <https://doi.org/10.1002/ecm.1331>
- Boddy, L. (2001). Fungal community ecology and Wood decomposition processes in angiosperms: From standing tree to complete decay of coarse Woody debris. *Ecological Bulletins*, 49, 43–56. <https://doi.org/10.2307/20113263>
- Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.
- Bouget, C., Brin, A., Tellez, D., & Archaux, F. (2015). Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. *Oecologia*, 177(3), 911–920. <https://doi.org/10.1007/s00442-014-3162-9>
- Bradford, M. A., Warren, R. J., II, Baldrian, P., Crowther, T. W., Maynard, D. S., Oldfield, E. E., Wieder, W. R., Wood, S. A., & King, J. R. (2014). Climate fails to predict wood decomposition at regional scales. *Nature Climate Change*, 4(7), 625–630. <https://doi.org/10.1038/nclimate2251>
- Brändle, M., & Brandl, R. (2001). Species richness of insects and mites on trees: Expanding Southwood. *Journal of Animal Ecology*, 70(3), 491–504.
- Burner, R. C., Stephan, J. G., Drag, L., Birkemoe, T., Muller, J., Snäll, T., Ovaskainen, O., Potterf, M., Siitonen, J., Skarpaas, O., Doerfler, I., Gossner, M. M., Schall, P., Weisser, W. W., & Sverdrup-Thygesen, A. (2021). Traits mediate niches and co-occurrences of forest beetles in ways that differ among bioclimatic regions. *Journal of Biogeography*, 48(12), 3145–3157. <https://doi.org/10.1111/jbi.14272>
- Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R., & Müller, J. (2011). Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. *Forest Ecology and Management*, 262(9), 1887–1894. <https://doi.org/10.1016/j.foreco.2011.08.011>
- Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology & Evolution*, 32(6), 429–437. <https://doi.org/10.1016/j.tree.2017.03.004>
- 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(1), 297–324. <https://doi.org/10.1146/annurev-ecolsys-120213-091540>
- Chao, A., Chiu, C. H., Wu, S. H., Huang, C. L., & Lin, Y. C. (2019). Comparing two classes of alpha diversities and their corresponding beta and

- (dis)similarity measures, with an application to the Formosan sika deer *Cervus nippon taiouanus* reintroduction programme. *Methods in Ecology and Evolution*, 10(8), 1286–1297. <https://doi.org/10.1111/2041-210X.13233>
- Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67.
- Chao, A., Ma, K. H., Hsieh, T. C., & Chiu, C. H. (2016). *Online program SpadeR (species-richness Prediction and diversity Estimation in R)*. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/
- Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), 2351–2363. <https://doi.org/10.1098/rstb.2011.0063>
- Clements, F. E. (1916). *Plant succession: An analysis of the development of vegetation*. Carnegie Institution of Washington.
- Dickie, I. A., Fukami, T., Wilkie, J. P., Allen, R. B., & Buchanan, P. K. (2012). Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecology Letters*, 15(2), 133–141. <https://doi.org/10.1111/j.1461-0248.2011.01722.x>
- Dray, S., Pélissier, R., Couteron, P., Fortin, M. J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A. B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257–275. <https://doi.org/10.1890/11-1183.1>
- Ferro, M. L. (2018). It's the end of the Wood as we know it: Insects in Veneris (highly decomposed) Wood. In M. D. Ulyshen (Ed.), *Saproxylic insects* (pp. 729–796). Springer.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Schulze, E.-D., & Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The biodiversity Exploratories. *Basic and Applied Ecology*, 11, 473–485.
- Friess, N., Müller, J. C., Aramendi, P., Bässler, C., Brändle, M., Bouget, C., Brin, A., Bussler, H., Georgiev, K. B., Gil, R., Gossner, M. M., Heilmann-Clausen, J., Isacsson, G., Krištín, A., Lachat, T., Larrieu, L., Magnanou, E., Maringer, A., Mergner, U., ... Seibold, S. (2019). The species-rich arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests. *Diversity and Distributions*, 25(5), 783–796. <https://doi.org/10.1111/ddi.12882>
- Fukami, T. (2015). Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>
- Fukami, T., Dickie, I. A., Wilkie, J. P., Paulus, B. C., Park, D., Roberts, A., Buchanan, P. K., & Allen, R. B. (2010). Assembly history dictates ecosystem functioning: Evidence from wood decomposer communities. *Ecology Letters*, 13(6), 675–684. <https://doi.org/10.1111/j.1461-0248.2010.01465.x>
- Gibb, H., Hjäältén, J., Ball, J. P., Pettersson, R. B., Landin, J., Alvin, O., & Danell, K. (2006). Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congeners? *Biological Conservation*, 132(2), 250–260. <https://doi.org/10.1016/j.biocon.2006.04.017>
- Goslee, S., & Urban, D. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22, 1–19.
- Gossner, M. M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K. E., Steffan-Dewenter, I., Schulze, E. D., & Weisser, W. W. (2016). Deadwood enrichment in European forests—Which tree species should be used to promote saproxylic beetle diversity? *Biological Conservation*, 201, 92–102. <https://doi.org/10.1016/j.biocon.2016.06.032>
- Gotelli, N. J., & Entsminger, N. J. (2003). Swap algorithms in null model analysis. *Ecology*, 84, 532–535.
- Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, 33(1), 1–23. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150507>
- Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H., Christensen, M., Gossner, M. M., Heilmann-Clausen, J., Horák, J., Gruppe, A., Isacsson, G., Köhler, F., Lachat, T., Larrieu, L., Schlaghamersky, J., Thorn, S., Zapponi, L., & Müller, J. (2019). Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *Journal of Biogeography*, 46(5), 1054–1065. <https://doi.org/10.1111/jbi.13556>
- Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H. B., Gossner, M. M., Gruppe, A., Heibl, C., Jarzabek-Müller, A., Seibold, S., Siitonen, J., Soutinho, J. G., Sverdrup-Thygeson, A., Thorn, S., & Drag, L. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *Journal of Animal Ecology*, 90, 1934–1947. <https://doi.org/10.1111/1365-2656.13512>
- Hanski, I. (1989). Fungivory: Fungi, insects and ecology. In N. Wilding, N. Collins, P. Hammond, & J. Webber (Eds.), *Insect-fungus interactions* (pp. 25–68). Academic Press.
- Harmon, M. E., Fasth, B. G., Yatskov, M., Kastendick, D., Rock, J., & Woodall, C. W. (2020). Release of coarse woody detritus-related carbon: A synthesis across forest biomes. *Carbon Balance and Management*, 15(1), 1–21. <https://doi.org/10.1186/s13021-019-0136-6>
- Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54(2), 427–432. <https://doi.org/10.2307/1934352>
- Jacobsen, R. M., Birkemoe, T., & Sverdrup-Thygeson, A. (2015). Priority effects of early successional insects influence late successional fungi in dead wood. *Ecology and Evolution*, 5(21), 4896–4905. <https://doi.org/10.1002/ece3.1751>
- Janssen, P., Fuhr, M., Cateau, E., Nusillard, B., & Bouget, C. (2017). Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, 205, 1–10. <https://doi.org/10.1016/j.biocon.2016.11.021>
- Jonsell, M., Abrahamsson, M., Widenfalk, L., & Lindbladh, M. (2019). Increasing influence of the surrounding landscape on saproxylic beetle communities over 10 years succession in dead wood. *Forest Ecology and Management*, 440, 267–284. <https://doi.org/10.1016/j.foreco.2019.02.021>
- Jonsell, M., & Nordlander, G. (2004). Host selection patterns in insects breeding in bracket fungi. *Ecological Entomology*, 29(6), 697–705. <https://doi.org/10.1111/j.0307-6946.2004.00654.x>
- Jonsell, M., Schroeder, M., & Weslien, J. (2005). Saproxylic beetles in high stumps of spruce: Fungal flora important for determining the species composition. *Scandinavian Journal of Forest Research*, 20(1), 54–62. <https://doi.org/10.1080/02827580510008211>
- Jonsell, M., Weslien, J., & Ehnstrom, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, 7(6), 749–764.
- Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K. E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., ... Gossner, M. M. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, 391, 86–95. <https://doi.org/10.1016/j.foreco.2017.02.012>
- Kahl, T., & Bauhus, J. (2014). An index of forest management intensity based on assessment of harvested tree volume, tree species

- composition and dead wood origin. *Nature Conservation*, 7, 15–27. <https://doi.org/10.3897/natureconservation.7.7281>
- Kennedy, C. E. J., & Southwood, T. R. E. (1984). The number of species of insects associated with British trees: A re-analysis. *The Journal of Animal Ecology*, 53(2), 455. <https://doi.org/10.2307/4528>
- Komonen, A., & Müller, J. (2018). Dispersal ecology of dead wood organisms: Implications for connectivity conservation. *Conservation Biology*, 32, 535–545.
- Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L., Inouye, B. D., Harrison, S. P., & Myers, J. A. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, 333(6050), 1755–1758. <https://doi.org/10.1126/science.1208584>
- Lasky, J. R., Uriarte, M., Boukili, V. K., & Chazdon, R. L. (2014). Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, 111(15), 5616–5621. <https://doi.org/10.1073/pnas.1319342111>
- Lassauce, A., Paillet, Y., Jactel, H., & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, 11(5), 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>
- Lee, S.-I., Spence, J. R., & Langor, D. W. (2014). Succession of saproxylic beetles associated with decomposition of boreal white spruce logs. *Agricultural and Forest Entomology*, 16(4), 391–405. <https://doi.org/10.1111/afe.12069>
- Leidinger, J., Blaschke, M., Ehrhardt, M., Fischer, A., Gossner, M. M., Jung, K., Kienlein, S., Kózak, J., Michler, B., Mosandl, R., Seibold, S., Wehner, K., & Weisser, W. W. (2021). Shifting tree species composition affects biodiversity of multiple taxa in central European forests. *Forest Ecology and Management*, 498, 119552. <https://doi.org/10.1016/j.foreco.2021.119552>
- Leidinger, J., Seibold, S., Weisser, W. W., Lange, M., Schall, P., Türke, M., & Gossner, M. M. (2019). Effects of forest management on herbivorous insects in temperate Europe. *Forest Ecology and Management*, 437, 232–245. <https://doi.org/10.1016/j.foreco.2019.01.013>
- Leidinger, J., Weisser, W. W., Kienlein, S., Blaschke, M., Jung, K., Kozak, J., Fischer, A., Mosandl, R., Michler, B., Ehrhardt, M., Zech, A., Saler, D., Graner, M., & Seibold, S. (2020). Formerly managed forest reserves complement integrative management for biodiversity conservation in temperate European forests. *Biological Conservation*, 242, 108437. <https://doi.org/10.1016/j.biocon.2020.108437>
- Li, S. P., Cadotte, M. W., Meiners, S. J., Pu, Z., Fukami, T., & Jiang, L. (2016). Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. *Ecology Letters*, 19(9), 1101–1109. <https://doi.org/10.1111/ele.12647>
- Lunde, L. F., Jacobsen, R., Kauserud, H., Boddy, L., Nybakken, L., Sverdrup-Thygesen, A., & Birkemoe, T. (2022). Legacies of invertebrate exclusion and tree secondary metabolites control fungal communities in dead wood. *Molecular Ecology*, 31(11), 3241–3253. <https://doi.org/10.1111/mec.16448>
- Maren, I. E., Kapfer, J., Aarrestad, P. A., Grytnes, J. A., & Vandvik, V. (2017). Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient. *Ecology*, 38, 42–49. <https://doi.org/10.1111/ijlh.12426>
- Meiners, S. J., Cadotte, M. W., Fridley, J. D., Pickett, S. T. A., & Walker, L. R. (2015). Is successional research nearing its climax? New approaches for understanding dynamic communities. *Functional Ecology*, 29(2), 154–164. <https://doi.org/10.1111/1365-2435.12391>
- Metcalfe, J. L., Xu, Z. Z., Weiss, S., Lax, S., Van Treuren, W., Hyde, E. R., Song, S. J., Amir, A., Larsen, P., Sangwan, N., Haarmann, D., Humphrey, G. C., Ackermann, G., Thompson, L. R., Lauber, C., Bibat, A., Nicholas, C., Gebert, M. J., Petrosino, J. F., ... Knight, R. (2016). Mammalian corpse decomposition. *Science*, 351(6269), 158–162. <https://doi.org/10.1126/science.aad2646>
- Michaud, J. P., Schoenly, K. G., & Moreau, G. (2015). Rewriting ecological succession history: Did carrion ecologists get there first? *Quarterly Review of Biology*, 90(1), 45–66. <https://doi.org/10.1086/679763>
- Moll, J., Heintz-Buschart, A., Bässler, C., Hofrichter, M., Kellner, H., Buscot, F., & Hoppe, B. (2021). Amplicon sequencing-based bipartite network analysis confirms a high degree of specialization and modularity for fungi and prokaryotes in deadwood. *mSphere*, 6(1). <https://doi.org/10.1128/msphere.00856-20>
- Möller, G. (2009). *Struktur- und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera—Käfer* (Dissertation at Freien Universität Berlin). Freie Universität Berlin.
- Mori, A. S., Fujii, S., Kitagawa, R., & Koide, D. (2015). Null model approaches to evaluating the relative role of different assembly processes in shaping ecological communities. *Oecologia*, 178(1), 261–273. <https://doi.org/10.1007/s00442-014-3170-9>
- Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, 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>
- Neff, F., Hagge, J., Achury, R., Ambarli, D., Ammer, C., Schall, P., Seibold, S., Staab, M., Weisser, W. W., & Gossner, M. M. (2022). Hierarchical trait filtering at different spatial scales determines beetle assemblages in deadwood. *Functional Ecology*, 975–982. <https://doi.org/10.1111/1365-2435.14186>
- Odum, E. P., & Odum, H. T. (1953). *Fundamentals of ecology*. Saunders.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2018). *Vegan: Community ecology package*. R package version 2.4–6.
- Ovaskainen, O., Hottola, J., & Shtonen, J. (2010). Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology*, 91(9), 2514–2521. <https://doi.org/10.1890/10-0173.1>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>
- Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.
- Payne, J. A., King, E. W., & Beinhart, G. (1968). Arthropod succession and decomposition of buried pigs. *Nature*, 219(5159), 1180–1181. <https://doi.org/10.1038/2191180a0>
- Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., Simons, N. K., Schall, P., van der Plas, F., Manning, P., Manzanedo, R. D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., ... Fischer, M. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecology Letters*, 22(1), 170–180. <https://doi.org/10.1111/ele.13182>
- Pulsford, S. A., Lindenmayer, D. B., & Driscoll, D. A. (2016). A succession of theories: Purging redundancy from disturbance theory. *Biological Reviews*, 91(1), 148–167. <https://doi.org/10.1111/brv.12163>
- Purahong, W., Wubet, T., Krüger, D., & Buscot, F. (2018). Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. *ISME Journal*, 12(1), 289–295. <https://doi.org/10.1038/ismej.2017.177>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>

- Rajala, T., Peltoniemi, M., Pennanen, T., & Mäkipää, R. (2012). Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. *FEMS Microbiology Ecology*, 81(2), 494–505. <https://doi.org/10.1111/j.1574-6941.2012.01376.x>
- Saint-Germain, M., Buddle, C. M., & Drapeau, P. (2010). Substrate selection by saprophagous wood-borer larvae within highly variable hosts. *Entomologia Experimentalis et Applicata*, 134, 227–233. <https://doi.org/10.1111/j.1570-7458.2009.00960.x>
- Schall, P., Schulze, E.-D., Fischer, M., Ayasse, M., & Ammer, C. (2018). Relations between forest management, stand structure and productivity across different types of central European forests. *Basic and Applied Ecology*, 32, 39–52. <https://doi.org/10.1016/j.baae.2018.02.007>
- Schmidl, J., & Bußler, H. (2004). Ökologische Gilden xylobionter Käfer Deutschlands. *Naturschutz Und Landschaftsplanung*, 36, 202–218.
- 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>
- Seibold, S., Bässler, C., Brandl, R., Gossner, M. M., Thorn, S., Ulyshen, M. D., & Müller, J. (2015). Experimental studies of dead-wood biodiversity—A review identifying global gaps in knowledge. *Biological Conservation*, 191, 139–149. <https://doi.org/10.1016/j.biocon.2015.06.006>
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., & Müller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29(2), 382–390. <https://doi.org/10.1111/cobi.12427>
- Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., Cadotte, M., Lindemayer, D. B., Adhikari, Y. P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R. S., Birkemoe, T., ... Müller, J. (2021). The contribution of insects to global forest deadwood decomposition. *Nature*, 597, 77–81. <https://doi.org/10.1038/s41586-021-03740-8>
- Sobek, S., Goßner, M. M., Scherber, C., Steffan-Dewenter, I., & Tschamtké, T. (2009). Tree diversity drives abundance and spatiotemporal β -diversity of true bugs (Heteroptera). *Ecological Entomology*, 34(6), 772–782. <https://doi.org/10.1111/j.1365-2311.2009.01132.x>
- Stokland, J., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in dead wood*. Cambridge University Press.
- Strong, D. R., Lawton, J. H., & Southwood, T. R. E. (1984). *Insects on plants. Community patterns and mechanisms*. Blackwell.
- Thorn, S., Chao, A., Bernhardt-Römermann, M., Chen, Y. H., Georgiev, K. B., Heibl, C., Müller, J., Schäfer, H., & Bässler, C. (2020). Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. *Ecology*, 101(3), 1–8. <https://doi.org/10.1002/ecy.2949>
- Turner, J. R. G. (2004). Explaining the global biodiversity gradient: Energy, area, history and natural selection. *Basic and Applied Ecology*, 5(5), 435–448. <https://doi.org/10.1016/j.baae.2004.08.004>
- Ulyshen, M. D. (2016). Wood decomposition as influenced by invertebrates. *Biological Reviews*, 91(1), 70–85. <https://doi.org/10.1111/brv.12158>
- Ulyshen, M. D. (2018). *Saproxylic insects diversity, ecology and conservation*. Springer. <https://doi.org/10.1007/978-3-319-75937-1>
- Ulyshen, M. D., & Hanula, J. L. (2010). Patterns of saproxylic beetle succession in loblolly pine. *Agricultural and Forest Entomology*, 12(2), 187–194. <https://doi.org/10.1111/j.1461-9563.2009.00467.x>
- Van Der Wal, A., Ottosson, E., & De Boer, W. (2015). Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology*, 96(1), 124–133. <https://doi.org/10.1890/14-0242.1>
- Vanderwel, M. C., Malcolm, J. R., Smith, S. A., & Islam, N. (2006). Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *Forest Ecology and Management*, 225(1–3), 190–199.
- Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E., & Thorn, S. (2021). Diversity and conservation of saproxylic beetles in 42 European tree species: An experimental approach using early successional stages of branches. *Insect Conservation and Diversity*, 14(1), 132–143. <https://doi.org/10.1111/icad.12442>
- Vogel, S., Gossner, M. M., Mergner, U., Müller, J., & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. *Journal of Applied Ecology*, 57(10), 2075–2085. <https://doi.org/10.1111/1365-2664.13648>
- Walker, L. R., & Wardle, D. A. (2014). Plant succession as an integrator of contrasting ecological time scales. *Trends in Ecology & Evolution*, 29(9), 504–510. <https://doi.org/10.1016/j.tree.2014.07.002>
- Weedon, J. T., Cornwell, W. K., Cornelissen, J. H. C., Zanne, A. E., Wirth, C., & Coomes, D. A. (2009). Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters*, 12(1), 45–56. <https://doi.org/10.1111/j.1461-0248.2008.01259.x>
- Welti, E. A. R., Zajicek, P., Frenzel, M., Ayasse, M., Bornholdt, T., Buse, J., Classen, A., Dziöck, F., Engelmann, R. A., Englmeier, J., Fellendorf, M., Förtscher, M. I., Fricke, U., Ganuza, C., Hippke, M., Hoenselaar, G., Kaus-Thiel, A., Kerner, J., Kilian, D., ... Haase, P. (2022). Temperature drives variation in flying insect biomass across a German malaise trap network. *Insect Conservation and Diversity*, 15(2), 168–180. <https://doi.org/10.1111/icad.12555>
- Wende, B., Gossner, M. M., Grass, I., Arnstadt, T., Hofrichter, M., Floren, A., Linsenmair, K. E., Weisser, W. W., & Steffan-Dewenter, I. (2017). Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. *Proceedings of the Royal Society B: Biological Sciences*, 284(1854), 20170198. <https://doi.org/10.1098/rspb.2017.0198>
- Weslien, J., Djupström, L. B., Schroeder, M., & Widenfalk, O. (2011). Long-term priority effects among insects and fungi colonizing decaying wood. *The Journal of Animal Ecology*, 80(6), 1155–1162. <https://doi.org/10.1111/j.1365-2656.2011.01860.x>
- Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309. <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>
- Wöllauer, S., Zeuss, D., Hänsel, F., & Naus, T. (2021). TubeDB: An on-demand processing database system for climate station data. *Computers and Geosciences*, 146, 104641. <https://doi.org/10.1016/j.cageo.2020.104641>
- Zuo, J., Berg, M. P., Van Hal, J., Van, R. S. P., Goudzwaard, L., Hefting, M. M., Poorter, L., Sterck, F. J., & Cornelissen, J. H. C. (2020). Fauna community convergence during decomposition of deadwood across tree species and forests. *Ecosystems*, 24, 926–938. <https://doi.org/10.1007/s10021-020-00558-9>

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How to cite this article: Seibold, S., Weisser, W. W., Ambarli, D., Gossner, M. M., Mori, A. S., Cadotte, M. W., Hagge, J., Bässler, C., & Thorn, S. (2023). Drivers of community assembly change during succession in wood-decomposing beetle communities. *Journal of Animal Ecology*, 92, 965–978. <https://doi.org/10.1111/1365-2656.13843>