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

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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

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 8years 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, 3–140 m a.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, 285–550 m a.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, 460–860 m a.s.l.). Annual precipitation ranged between 500 and 1000 mm and mean annual temperature between 6 and 8.5C° 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 un-managed beech forest (3 plots; unmanaged for at least 20 years), 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. 35 cm 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 100 m × 100 m between 2008 and 2011. Canopy cover was assessed by airborne LiDAR during leaf-on conditions (HAI: 2008; SCH, ALB: 2009) for a 20 m 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 characterizes 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.
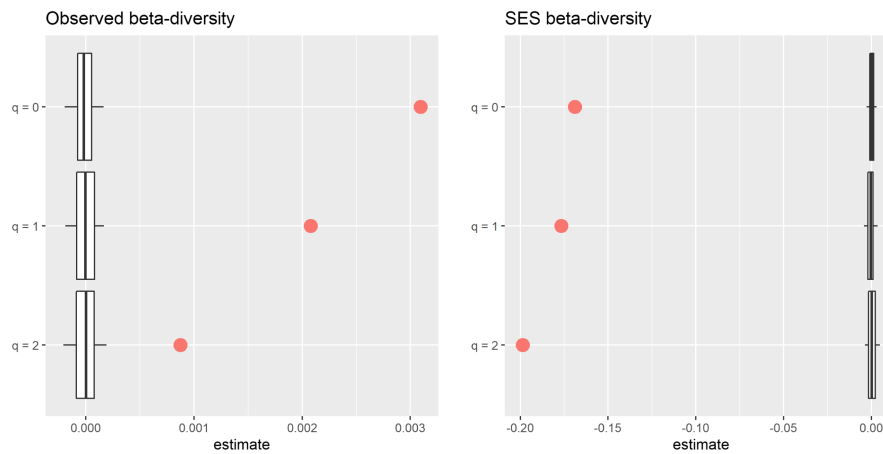
FIGURE 1 Linear coefficients of the effect of year on observed values (left) and standardized effect size (SES; right) of spatial beta-diversity of saproxylic beetles between logs within years along the series of Hill numbers ($q = 0$–2). Red circles indicate coefficients of models for observed data 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 ($p > 0.05$).
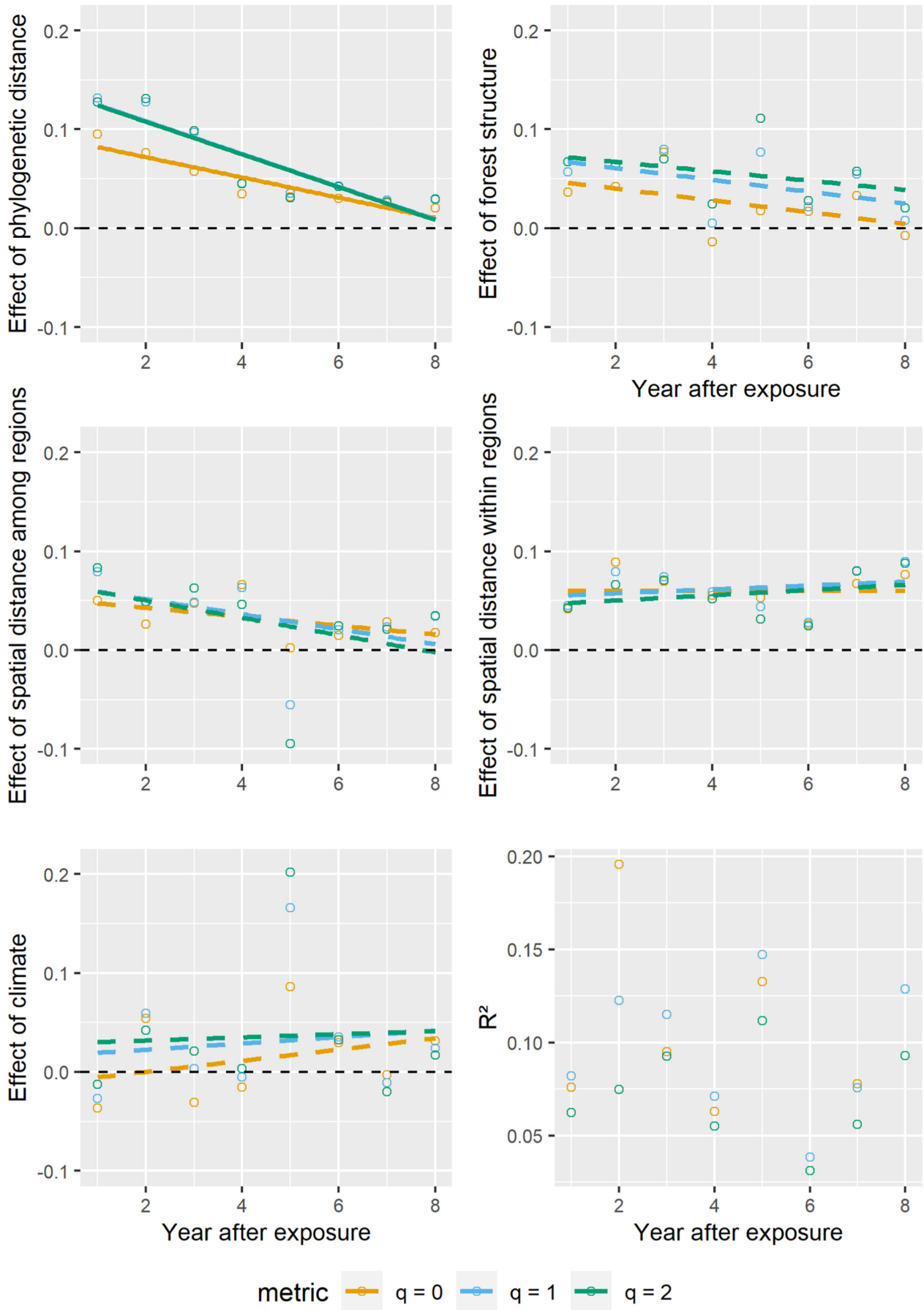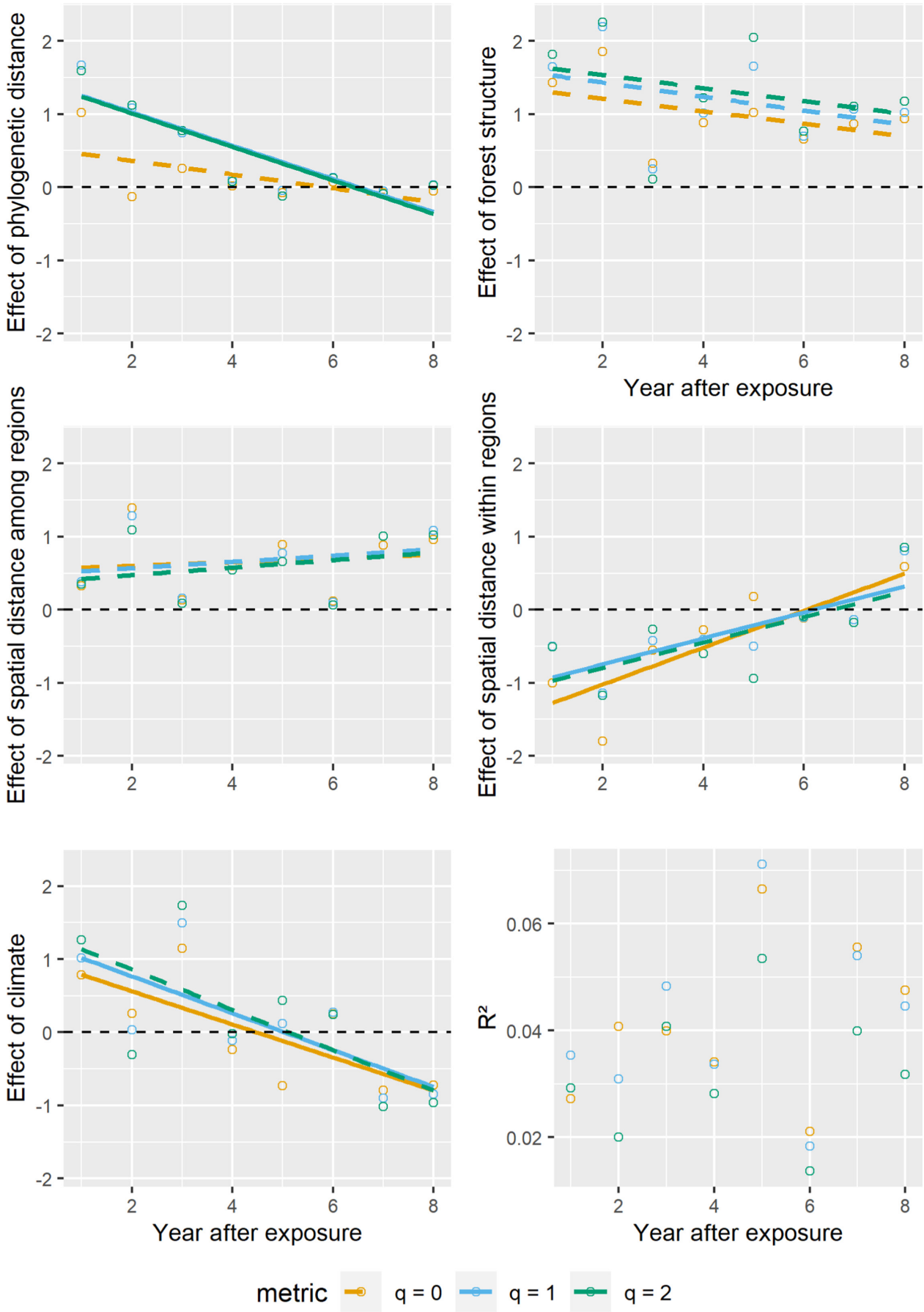
FIGURE 3 Temporal change in *F*-values indicating the effect size of drivers of standardized effect sizes (SES) of spatial beta-diversity between logs within years. Circles show *F*-values of MRM-analyses of SES beta diversity values along the series of Hill numbers against three predictor dissimilarity 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 that 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.

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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