Drivers of community assembly change during succession in wood-decomposing insect 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 along faunal succession 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 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 eight years of wood decomposition. Our study included 379 experimental deadwood logs comprising 13 different tree species in 30 forest stands in Germany with differences in forest structure that is influenced by management regimes. We hypothesized that the effect of tree species dissimilarity, measured by phylogenetic distance, on spatial beta-diversity decreases over time, while the effects of spatial distance between logs (1m to ~600km) and differences in forest structure increase.
4. Spatial beta-diversity of saproxylic beetle communities was high throughout the first eight years of succession and even increased slightly over time except when focusing on dominant species (i.e., $q = 2$ in the Hill number calculation). Beta-diversity increased with increasing phylogenetic distance between tree species, spatial distance, and differences in forest structure. While effects of space and forest structure were constant over time, the effect of phylogenetic distance decreased over time.

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 between 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 promoted by high diversity in tree species and forest structural characteristics.

Keywords

beetle, deadwood, decomposition, forest management, saproxylic, succession

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, Cadotte, Fridley, Pickett, & Walker, 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, Uriarte, Boukili, & Chazdon, 2014; Li et al., 2016; Maren, Kapfer, Aarrestad, Grytnes, & Vandvik, 2017; Meiners et al., 2015; Walker & Wardle, 2014), but is no less important for ecosystem functioning. Decomposer succession coincides with a predictable decrease 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, King, & Beinhart, 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), and it is not clear if the same predictability applies.

Deadwood is key habitat for biodiversity in forest ecosystems (Stokland, Siitonen, & Jonsson, 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 beetles 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 beetles and to maintain the ecosystem function they provide in forests, a better understanding of the drivers of community assembly of saproxylic beetles is needed.

Many saproxylic beetle species have adapted to the chemical and physical characteristics of their host tree species (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 in saproxylic insect communities decreases with ongoing succession (Ulyshen & Hanula, 2010). This process should lead to biotic homogenisation over time, exhibited by decreasing spatial beta-diversity, as measured by the dissimilarity in species composition between saproxylic beetle 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 beetle 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 of saproxylic beetles even if secondary compounds dissipate.

Furthermore, saproxylic beetle communities depend not only on wood characteristics associated with tree species but also on the composition of preceding insect communities (Jacobsen, Birkemoe, & Sverdrup-Thygeson, 2015; Weslien, Djupström, Schroeder, & Widenfalk, 2011). Such priority effects of early- on late-successional species 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), but 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.

The composition of saproxylic insect communities varies geographically, presumably reflecting spatial variation in environmental conditions and dispersal limitation, and thus beta-diversity increases with increasing spatial distance between deadwood logs (Bae et al., 2020; Müller et al., 2020). Moreover, saproxylic insect communities can be strongly influenced by management-related forest structural changes, such as changes to canopy cover, tree species composition and deadwood amount in a stand (Hagge et al., 2019; Seibold, Bässler, et al., 2015). It has been shown that at the regional level (~20 km), differences in forest structure 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, Gossner, Mergner, Müller, & Thorn, 2020). Characteristics of saproxylic beetle species associated with spatial processes (e.g. dispersal ability) and forest structure (Bouget, Brin, Tellez, & Archaux, 2015; Gibb et al., 2006) likely change with succession and it stands to reason that the effect of spatial distance and forest structure on spatial beta-diversity between logs is expected to change accordingly. Considering for example that early successional species are better dispersers than late successional species (Ulyshen & Hanula, 2010), the effect of spatial distance and forest management on beta-diversity of saproxylic beetle communities should increase, but data are lacking.

To study drivers of community assembly of saproxylic beetles along succession, 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 ~600 km 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 eight years of succession (2010 to 2017). To evaluate how the effects of tree species differences (quantified as phylogenetic distance between tree species), spatial distance between deadwood logs (1 m to ~600 km) 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, & Jost, 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, Fujii, Kitagawa, & Koide, 2015) by comparing observations to a null expectation of beta-diversity. In particular, we tested the following hypotheses:

H1: Spatial beta-diversity of beetle communities decreases over time due to biotic homogenization of resources in the process of deadwood decomposition.

H2: 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.

H3: Spatial beta-diversity increases with increasing spatial distance between deadwood logs and differences in forest structure and both effects increase with ongoing succession.

Methods

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, about 420 km^2, 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 unmanaged 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 set up 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 approx. 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.

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 & Bußler (2004).

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, Schulze, Fischer, Ayasse, & Ammer, 2018) and a deadwood inventory (Kahl & Bauhus, 2014) was conducted on all plots covering an area of 100 m x 100 m. 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). Forest structures did not change strongly over time and thus the same forest structure data were used to characterizes differences between plots for all years.

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, Chiu, Wu, Huang, & Lin, 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, i.e. 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, Ma, Hsieh, & Chiu, 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.

Statistical analyses

Statistical analyses were conducted in R version 4.0.3 (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, Maechler, Bolker, & Walker, 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. The identity of both logs included in respective comparisons were included as separate random effects to account for repeated measures.

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 phylogenetic distance between host tree species, spatial distance between logs and dissimilarity based on forest structures as explanatory dissimilarity matrices, with each matrix standardized to range of 0 – 1. The phylogenetic distance matrix was calculated using the function *cophenetic.phylo* in the package *ape* (Paradis & Schliep, 2019). Spatial distances were calculated as distance between coordinates using the function *pointDistance* in package *raster*. Dissimilarity based on forest structure was based on basal area, proportion of basal area represented by conifers, number of tree species, deadwood volume and canopy cover and calculated as Euclidean distance based on standardized variables (range 0 – 1) using the function *vegdist* in the package *vegan* (Oksanen et al., 2018). 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 change over time by including the year as continuous variable (1 – 8) as explanatory variable.

Results

Over eight 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 q = 0 and q = 1, but did not change for q = 2, which reflects when mostly the dominant species are considered (Fig. 1; Table S1). The standardized effect size (SES) of spatial beta-diversity decreased significantly over time indicating higher dissimilarity than expected in early years, but the coefficients of these effects were small and mainly driven by the first two years (Fig. 1; Table 1).

Observed spatial beta-diversity and the SES of spatial beta-diversity along the series of Hill numbers increased with increasing phylogenetic distance between tree species, spatial distance between deadwood logs and dissimilarity with regard to forest structure (i.e., canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume; Fig 2. and Fig. S1, Table S2). The effect of phylogenetic distance decreased over time for observed spatial beta-diversity and SES of spatial beta-diversity along the Hill series (Fig. 2 and Fig. S1). The effects of spatial distance and dissimilarity in forest structure did not change significantly over time.

Discussion

Patterns of spatial beta-diversity over a time series of eight years indicate that assembly patterns of saproxylic beetle communities change with faunal succession. Inconsistent with our first hypothesis, observed beta-diversity increased over time, except for dominant species. Yet, the null-model approach showed that beta-diversity was higher than expected in early years but less so from year three to eight. Spatial beta-diversity was driven by phylogenetic distances between tree species, spatial distances between deadwood logs and forest structure. 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 was that the influence of space and forest structure remained constant over time.

Succession of decomposer communities in deadwood is associated with changes in wood characteristics and decreasing resource availability (Lee, Spence, & Langor, 2014; Stokland et al., 2012; Ulyshen & Hanula, 2010; Zuo et al., 2020). We hypothesized that spatial beta-diversity of saproxylic beetle communities decreases over time as tree-species specific differences in wood characteristics decrease. In contrast to our expectation, observed beta-diversity increased for Hill numbers $q = 0$ and $q = 1$ and did not change for $q = 2$, indicating that rare species contribute 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, particularly in the first two years. High standardized effect sizes of beta-diversity can result from rare species occurring in few samples, or of abundant species with a high chance to appear in null-model communities, leading to small standard deviation and thus high standardized effect sizes. Early saproxylic beetle communities include rare, specialized species, as well as some highly abundant species of which some a 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 two years in our samples. Considering that observed beta-diversity increased over time for q = 0 and q = 1, abundant but specialized species are most likely the reason why beta-diversity was higher than expected by chance during early years of succession. In contrast, high observed beta-diversity during later years of succession are likely driven by rare species. This finding indicates an increasing importance of stochasticity over time (Meiners et al., 2015; Pulsford, Lindenmayer, & Driscoll, 2016).

Observed and standardized effects size of beta-diversity were influenced by phylogenetic distances between tree species which is consistent with earlier studies focusing on early stages of saproxylic beetle succession (Müller et al., 2020; Vogel et al., 2020). In line with our expectation, the effect of phylogenetic distances between tree species on beta-diversity decreased over time and was not significant in later years. This pattern is likely associated with differences in wood traits, such as secondary compounds, which characterize differences between tree species particularly during early stages of decay when the bark is present (Dossa et al., 2018). 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).

There are several potential explanations for high values of observed spatial beta-diversity during later successional stages. Decomposition rates vary between tree species but also between logs of the same tree species and even within single logs (Kahl et al., 2017; Saint-Germain, Buddle, & Drapeau, 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, Malcolm, Smith, & Islam, 2006) and since fungal biomass and diversity increase over time (Boddy, 2001; Rajala, Peltoniemi, Pennanen, & Mäkipää, 2012), high spatial beta-diversity 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, Ottosson, & De Boer, 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, i.e. via priority effects (Fukami, 2015). Priority effects have been documented for saproxylic communities in both laboratory experiments (Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012; Fukami et al., 2010) and field experiments (Jacobsen et al., 2015; Weslien et al., 2011).

Spatial distance between deadwood logs affected spatial beta-diversity for all values of the q parameter and these effects were stable along the successional gradient. Compared to Müller et al. (2020) who found only weak effects of space on saproxylic beetle diversity at a regional scale (~20 km), our study covered a larger spatial gradient (~ 600 km) and more pronounced differences in biogeography and climate (Fischer et al., 2010). This suggests that processes related to spatial distance, such as dispersal and biogeography, structure the saproxylic beetle communities mainly at larger spatial scales (Bae et al., 2020; Komonen & Müller, 2018). Forest structure and composition, such as canopy cover, deadwood amount and tree species composition, determine habitat availability and quality and are thus important drivers of saproxylic beetle communities (Janssen, Fuhr, Cateau, Nusillard, & Bouget, 2017; Leidinger et al., 2020; Seibold et al., 2016). In line with these studies, our results show that beta-diversity of saproxylic beetle communities can be partially explained by forest structure, slightly more strongly for abundant and dominant species than rare species. Studies assessing whether effects of forest structure on saproxylic beetle communities change with faunal succession are missing. 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.

Conclusions

Based on data covering eight 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, beta-diversity was high throughout. Potential processes 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 spatial distance between deadwood logs and forest structure with their effects being stable over time. 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 species. Moreover, saproxylic beetle biodiversity benefits from variation in forest structure, e.g. in canopy cover or basal area, and thus structural heterogeneity should be promoted at the landscape scale. Finally, positive effects of spatial distance between deadwood logs on beta-diversity of saproxylic beetle communities indicate that conservation efforts should cover larger spatial extends to capture variation in environmental conditions.

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Data availability

Data are available from the Biodiversity Exploratories Information System (https://doi.org/10.17616/R32P9Q) at https://www.bexis.uni-jena.de with dataset IDs 24546, 18270 and 30925 for forest structure and 31123 for saproxylic beetles.

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Figure legends:

Figure 1: Temporal patterns of spatial beta-diversity between logs within years showing observed values and standardized effect size (SES) of beta-diversity of saproxylic beetles along the series of Hill numbers ($q = 0$ to 2). Regression lines were derived from linear mixed models with random effects for log IDs which were included in each pairwise comparison to account for multiple comparisons. Models included year as continuous variable, but data are depicted by boxplots for a better representation of their distribution. Dashed lines indicate non-significant relationships ($p > 0.05$).

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, on spatial distance and the differences in forest structure (i.e. canopy cover, basal area, proportion of conifer species, number of tree species and deadwood volume). Regression lines were derived from linear models. Dashed lines indicate non-significant relationships ($p > 0.05$).

Figure 1:

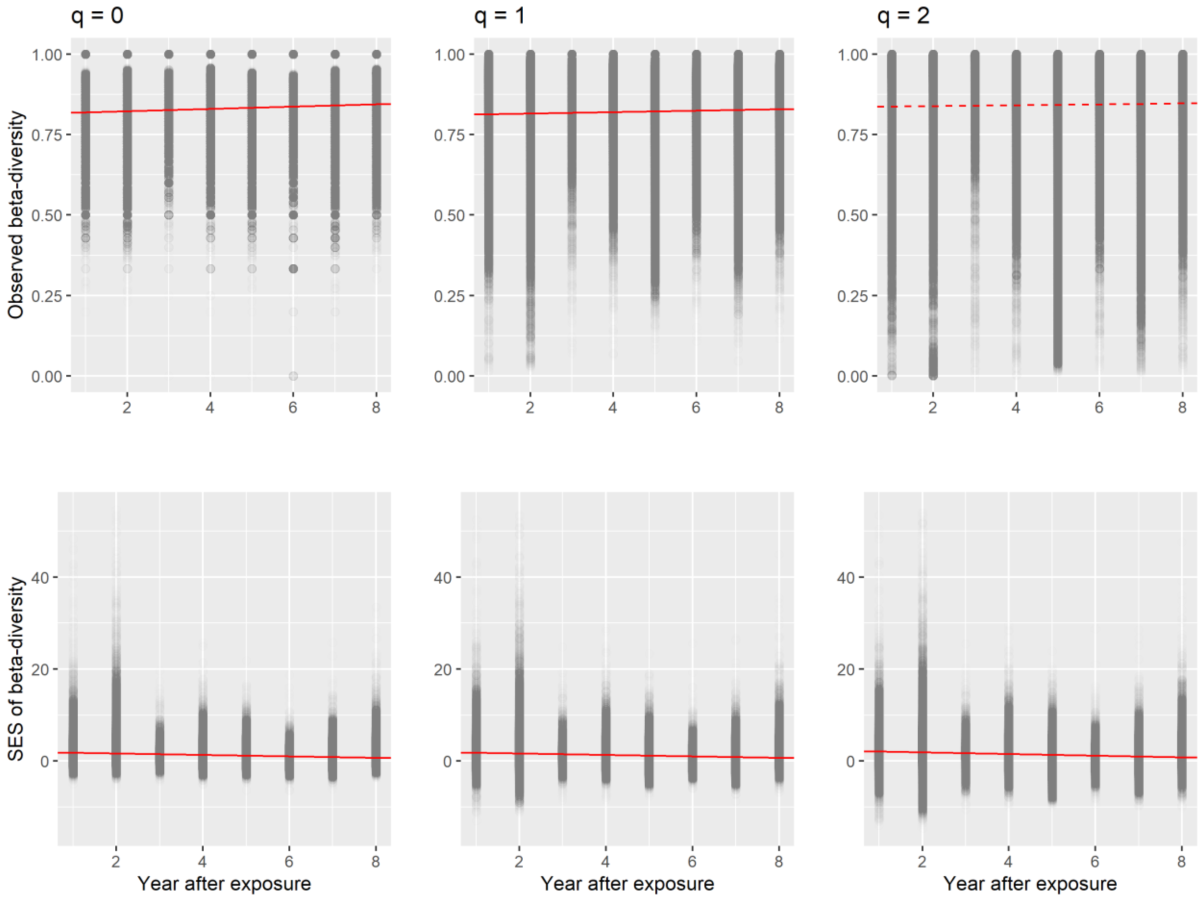
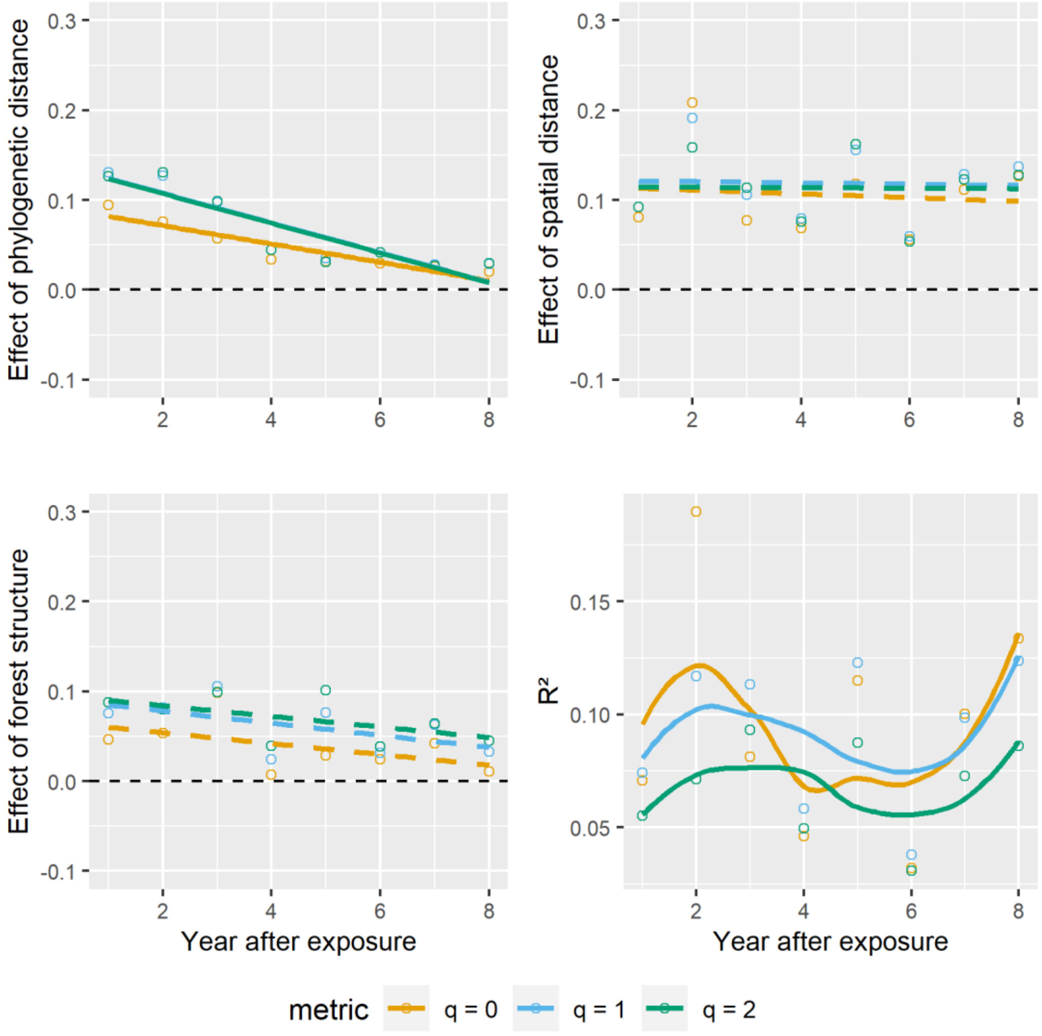

q = 0
q = 1
q = 2
Observed beta-diversity
1.00
0.75
0.50
0.25
0.00
2
4
6
8
SES of beta-diversity
40
20
0
Year after exposure
Year after exposure
Year after exposure

Figure 2:


Effect of phylogenetic distance
Effect of spatial distance
Effect of forest structure
R²
0.3
0.2
0.1
0.0
-0.1
0.15
0.10
0.05
2
4
6
8
Year after exposure
metric
q = 0
q = 1
q = 2