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The importance of heterogeneity revisited from a multiscale and multitaxa approach

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ABSTRACT

The importance of spatial scale for β-diversity has been shown in several studies, but it is unclear how spatial diversity patterns correlate among different organismic groups. We studied spatial diversity organization of plants and several trophic guilds of beetles in beech-dominated forests in two regions of Germany to test whether different trophic guilds are organized independently in space. We applied multiplicative diversity partitioning using a nested hierarchical design of four increasingly broader spatial levels (subplot, plot, forest class, region) and tested for correlations among trophic guilds by using Pearson product moment correlations and Mantel-tests. We observed similar general diversity patterns at different trophic guilds showing a high contribution of β-diversity to total γ-diversity and found β-diversity to be higher at different spatial scales and α-diversity to be lower than expected by random distributions of individuals. Results, however, partly depended on the weighting of rare and abundant species. Beta-diversity in our study was caused mainly by species spatial turnover rather than by nestedness. Correlations of α-diversity between trophic guilds were low whereas correlations of β-diversity above subplot level were high. Importantly, more strongly connected trophic guilds revealed not generally stronger relationships than less strongly connected guilds. Three important implications for conservation can be deduced from our results: (1) heterogeneity of beech forests at different spatial scales should be supported in conservation strategies to enhance biodiversity and related functions; (2) the observed high importance of spatial turnover in relation to nestedness implies a concentration of conservation efforts to a large number of not necessarily the richest sites, and (3) recommendation for particular conservation strategies (e.g. selection of priority sites for conservation at regional scale) based on single indicator taxa or functional guild is difficult because of the varied response of the species in our study.

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1. Introduction

Conserving biodiversity requires detailed knowledge of how diversity is distributed within and between habitats. Starting from Whittaker (1960), an increasing number of studies has emphasized the importance of compositional heterogeneity between places, or beta-diversity, for total biodiversity (gamma-diversity) in a region (Gossner and Müller, 2011; Hirao et al., 2007; Müller and Gossner, 2010; Summerville et al., 2003). Beta-diversity has been shown to be important for understanding broad bio-geographical diversity patterns such as elevational, latitudinal and longitudinal gradients (Kraft et al., 2011; Qian et al., 2005). If β-diversity is high, site selection for conservation presents a formidable challenge. For example, for beech forests and for headwater streams it is crucial to consider complementarity in species composition in the selection of conservation target sites as β-diversity contributes greatly to overall diversity (Clarke et al., 2010; Müller et al., 2013). Clough et al. (2007) showed that conservation-orientated evaluation of management schemes in agricultural landscapes needs to include β-diversity, because of its contribution to total diversity at the landscape scale. Importantly, however, measures of species diversity including β-diversity are dependent on the spatial scale considered (Gabriel et al., 2006; Gossner and Müller, 2011;

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Tuomisto, 2010a, 2010b). While the β-diversity fraction of overall diversity tends to increase with an increase in the spatial scale considered (Crist and Veech, 2006; Crist et al., 2003; Gabriel et al., 2006), significant species turnover might also occur at small spatial scales where it is particularly relevant for local conservation efforts (Müller and Gossner, 2010). While most studies have considered patterns of β-diversity across large geographic scales, some have studied β-diversity from local to landscape scale, often across gradients of land-use intensity (Dormann et al., 2007; Gabriel et al., 2006; Lawton et al., 1998).

The importance of β-diversity for total biodiversity may also be different for different taxa, depending upon whether the main drivers of species occurrences within sites differ among taxa. Most previous studies on spatial diversity partitioning have, however, focused either on a single (Summerville et al., 2003) or two (Hirao et al., 2007) taxa or on a single guild (e.g. saproxylic beetles, Müller and Gossner, 2010). When several taxa are studied simultaneously, the relative importance of β-diversity for different groups can be assessed. Such studies are rare. Comparing four plant and eight animal groups in rainforest and agroforestry sites in Sulawesi, Indonesia, Kessler et al. (2009) found that while different taxa had largely independent patterns of α-diversity, patterns of β-diversity were more congruent. Overall, α-diversity could not be used to predict β-diversity neither within nor between taxonomic groups, emphasizing the need to study species turnover between sites separately for each taxon. Thus, patterns of β-diversity may vary between different taxa, but it is unclear if there are systematic differences with respect to different ecological groupings such as differences between plants and animals, or between different trophic levels (Kessler et al., 2009; Prendergast et al., 1993). Summerville et al. (2006), for instance, showed in their study on forest moths in North America that generalists exhibited higher levels of α-diversity, whereas β-diversity was more important in specialists. Their interpretation was that for specialists, patterns of distribution are dominated by intraspecific aggregation and substantial species turnover between forest stands owing to a patchy distribution of host resources. For the generalists they proposed stronger fluctuations in population size and smaller ranges than predicted by host species distribution as possible mechanisms for the higher importance of α-diversity. In a study on saproxylic beetle and true bug communities in temperate forests of Germany, Gossner and Müller (2011) found that for specialists β-diversity at the ecoregion level, the largest spatial scale considered, was greater than for generalist species. In general, however, there are few comparisons for patterns of β-diversity at different spatial scale for different ecological groups.

Studies of α- and β-diversity across different spatial scales or taxa have also been hindered by recent discussions on the different ways in which β-diversity may be computed, for example to address the mathematical dependency of measures of β-diversity on local α-diversity (see e.g. Veech and Crist, 2010 and paragraph 'Diversity partitioning' in the Method section). Another important point is the relative weight given to the relative abundances of species. Measures of β-diversity can be computed based on species occurrences, to weigh rare and abundant species equally, or they can include species abundances, yet those different measures are generally difficult to compare. The recent introduction of a general q-metric based on multiplicative partitioning (Jost, 2007) has improved the possibilities for calculating β-components along a continuous gradient of increasing weights of abundant species. This could be important for biodiversity conservation because conserving abundant species could be critical for conserving ecosystem functions (Gaston, 2010; Taylor et al., 2006).

Beta-diversity reflects two different phenomena, spatial turnover and nestedness, and all communities that are not identical in species can be described by one of these or a combination of both (Baselga, 2010). Spatial turnover describes the replacement of species by others and this might be either a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005). On the other hand, a community with fewer species may reflect a subset of a community with more species and thus observed β-diversity might be solely explained by nestedness. This reflects a non-random process of local 'species loss' with different possible underlying mechanisms (e.g. extinction, dispersal limitations; Ulrich et al., 2009). Disentangling these effects is crucial in order to better understand the observed β-diversity patterns and their causes. This is also essential for conservation purposes because a high nestedness would favor a conservation strategy prioritizing a small number of sites with high diversity whereas a high spatial turnover would require concentration of conservation efforts to a large number of not necessarily the richest sites (Wright and Reeves, 1992).

The aim of our study was to analyze differences in diversity partitioning from small (subplot) to regional scale between plants and different insect functional groups in temperate beech forests, which traditionally have been considered to be very homogeneous. Europe has a global responsibility to protect the biodiversity of beech forests and thus a better understanding of spatial β-diversity in different organisms will be crucial for improving conservation theory and practice (see e.g. Barton et al., 2013). We focused on plant and beetle communities of 35 forest sites in two regions in Germany and selected beetles as a target group because beetles are species rich and represent several trophic levels from decomposers to predators. Likewise, we selected vascular understorey plants as surrogate for the producer level because this forest stratum contains various species with different growth forms, dispersal modes, shade tolerances, and competitive strategies (Getzin et al., 2012). We expect that the wide variety of functional groups analyzed will allow us to find more general spatial β-diversity pattern which is mandatory for improving conservation strategies. We asked whether γ-diversity of different trophic guilds is similarly partitioned into independent α- and β-components. We hypothesized that (H1) β-diversity generally contributes more to γ diversity than α-diversity and this applies also at small spatial scales such as subplots within forest stands or forest plots within a forest landscape due to high structural heterogeneity, (H2) spatial turnover of species is more important in explaining β-diversity than nestedness due to the great importance of environmental filtering or spatial and historical constraints, (H3) patterns of β-diversity with respect to the contribution to total γ-diversity are more similar between trophic guilds with a direct feeding link than among those where there is no such direct link, e.g. patterns of plant β-diversity should be more similar to patterns in herbivore diversity than to those of predators. We also hypothesized that (H4) α-diversity and β-diversity at the lower spatial scales are more strongly correlated among trophic guilds with direct feeding links (e.g. plants and herbivores) than between those that are linked indirectly (e.g. plants and predators).

2. Materials and methods

2.1. Study sites

The study was conducted in the Hainich-Dün (10°10′24″–10°46′45″E, 50°56′15″–51°22′43″N) in Central Germany and in the Biosphere Reserve Schwäbische Alb (09°12′13″–09°34′49″E, 48°21′00″–48°32′04″N) in South Germany, within the framework of the Biodiversity Exploratories project (for details see Supplementary S1 and Fischer et al., 2010).

For this study, 35 beech forest experimental plots (henceforth 'plot') of 100 × 100 m were selected from the study sites of the

biodiversity exploratories (location of plots is shown in Fig. S1-1, Supplementary S1). In each plot, seven randomly distributed $10 \, m \times 10 \, m$ subplots were installed (mean distance = 31.06 m ± 3.23 SD). Plots were divided into three 'forest classes' depending on stand openness, as surrogate for structural variation, because the amount of light that reaches the forest floor is one of the main drivers of plant and insect diversity in the herb layer of forests (e.g. Gossner, 2009; Tinya et al., 2009). We classified stand openness as the total gap fraction derived from hemispherical photographs taken in the center of the seven $10 \, m \times 10 \, m$ subplots (Table S2-1 of Supplementary S2, see also Getzin et al., 2012). Diversity partitioning was studied among four hierarchical levels: region (N = 2, Schwäbische Alb, Hainich-Dün), forest class (N = 3), plot (N = 35, 10,000 m²), and subplot (N = 245, 100 m²).

2.2. Biodiversity assessment

2.2.1. Plant and beetle sampling

For each of the seven subplots of each plot all species of herbs, graminoids, ferns, and woody plants up to a height of 1.5 m were recorded, as well as their crown projection cover. Due to different stratification levels of different taxa within this height, the total crown projection cover may partly exceed 100%. During a less intensive examination of the plot area outside the sampling units we only rarely found species not recorded within the subplots.

For beetle sampling we used flight-interception traps consisting of a crossed pair of transparent plastic shields (40 cm × 60 cm), one in the center of each three out of the seven subplots. Beetles were trapped over one entire vegetation period (April to October 2008). Hence, each sample represents the community of a whole year. Traps were installed in the understorey (height: 1.5 m). All adult beetles were identified to species level by taxonomic specialists. Plants were assessed on seven subplots while beetles were sampled on three subplots only. Thus results might be biased by different sample size. To test this, all analyses were additionally performed based on three randomly chosen subplots per plot of the plant survey. In all cases results remained similar. Nevertheless, we present both results either in the main part (three subplots) or in the Supplementary (seven subplots).

2.2.2. Classification into trophic guilds

Organisms were classified into five trophic levels: plants, herbivores, fungal eaters (mycetophages), true predators and detritivores. Herbivores were further divided into xylophages, i.e. wood-eating species and other herbivores. Detritivores were divided into feces-feeding (coprophages), carcass-feeding (necrophages) and plant detritus-feeding (saprophages) species. Classification of beetles was based on the main feeding source during their whole life cycle (see Supplementary S7 for a complete list of species and assignment to trophic level/feeding guild). We henceforth use the term 'trophic guilds' for the eight different trophic levels/feeding guilds. Data on the feeding ecology of beetles was provided by specialists based on Böhme (2005).

2.3. Data analyses

2.3.1. Diversity partitioning

Gamma-diversity can be partitioned into α- and β-diversity components either additively (Veech et al., 2002), as done in most previous studies, or multiplicatively (Jost, 2007; Whittaker, 1960). Jost and colleagues (Jost, 2006, 2007; Jost et al., 2010) recommend the use the multiplicative approach because of the dependency of β-diversity on the α-diversity in additive partitioning. However, as demonstrated in a Forum in Ecology (Veech and Crist, 2010), neither the additive nor the multiplicative approach is able to produce

a β-diversity statistically independent of the α-diversity, as suggested by Jost (2006, 2007), Tuomisto and Ruokolainen (2006), and Jost et al. (2010). After inspecting all arguments offered in this forum and previous publications and owing to the advantages of using true diversities and q-metric (see below), which are implemented in the approach advocated by Jost (2006, 2007), we decided to use the multiplicative approach, based on Whittaker's (1960) formula:

$$\gamma = \alpha_1 \text{ (within subplot)} \times \beta_1 \text{ (among subplots)}$$
$$\times \beta_2 \text{ (among plots)} \times \beta_3 \text{ (among forest classes)}$$
$$\times \beta_4 \text{ (among regions).} \tag{1}$$

Another important point is the relative weight given to the relative abundances of species. Measures of β-diversity can be computed based on species occurrences, to weigh rare and abundant species equally, or they can include species abundances, yet those different measures are generally difficult to compare. By using q-metrics (based on Hill numbers, Hill, 1973) β-components can be calculated along a continuous gradient of increasing weight given to abundant species (Jost, 2007). The parameter q determines the sensitivity of the measure to the relative frequencies of species and is based on the so-called numbers equivalency, and ensures that the diversity of a community A with twice as many species as community B, with all species in both communities being equally abundant, is also twice as high as would be intuitively expected from a measure of diversity (Jost, 2006). We used the q-metric to analyze diversity patterns with different weighting of rare and abundant species by using three different q-values: (1) q = 0 corresponds to species richness; rare and abundant species in the community are equally weighted here; (2) q = 0.999 (and not q = 1, which would require division by zero) corresponds to the exponential of Shannon entropy; here, species are weighted in proportion to their frequency in the sampled community and thus it can be interpreted as the number of 'typical species' in the community; and (3) q = 2 corresponds to the inverse Simpson concentration; here, abundant species are favored and rare species are discounted and thus it can be interpreted as the number of 'very abundant species' in the community (see also Chao et al., 2012). For formula see Supplementary S3.

We multiplicatively partitioned the community of all trophic guilds using the software PARTITION 3.0 (Veech and Crist, 2009) without sample weighting.

The statistical significance of level-specific α and β estimates was tested using an unrestricted individual-based randomization procedure which is implemented in the PARTITION program (Veech and Crist, 2009). In this process 10,000 random distributions of species among samples were generated at all hierarchical levels. Each of the original level-specific estimates was then compared with the appropriate null distribution and used to test the null hypothesis that the observed α- and β-diversity are obtained by a random distribution of individuals among samples at all hierarchical levels. Statistical significance was assessed by the proportion of null values that are greater than (or smaller than) the actual estimate (Manly, 1997; Roff, 2006).

Baselga (2010) provide a method allowing to additively partition β-diversity into the two separate components of spatial turnover and nestedness. We used this method to test if differences in species richness might have biased our observed spatial diversity pattern. We assessed the overall multiple-site dissimilarity, considering the total β-diversity (Sørensen dissimilarity), as well as the spatial turnover (measured as Simpson dissimilarity) and nestedness (measured as nestedness-resultant fraction of Sørensen dissimilarity) components separated by trophic guild and region. We used the multiple-site generalizations of Sørensen and Simpson dissimilarity measures because they have

proved to efficiently discriminate turnover from nestedness (Baselga, 2010; Baselga et al., 2007). Details are given in Supplementary S5. We additionally used resampling ($N = 999$) of 10 plots per run to calculate multiple-site dissimilarities in order to account for differences in the number of plots in the two regions (Schwäbische Alb 15, Hainich-Dün 20). We performed these analyses by using the betapart package (function *beta.sample*) (Baselga and Orme, 2012) within the software R 2.14.0 (R Development Team, 2011).

2.3.2. Correlation of α-diversity and β-diversity among trophic guilds

We carried out correlation analyses for the subplot and plot level, but not for forest classes and regions, because of the low number of replicates.

We used the reciprocal Simpson index, which is the transformation of Simpsons α-diversity to true diversities, as proposed by Jost (2006, 2007) using the vegan package (Oksanen et al., 2012) in R. We calculated the Simpson-Index for each subplot ($N = 105$ or 245) and plot ($N = 35$) and tested for correlations among trophic guilds using two different analyses; (1) we used Pearson's product moment correlations ($N = 105$ replicates at subplot and $N = 35$ replicates at plot level for each correlation) to test if subplots or plots with a high α-diversity in one trophic guild also have a high α-diversity in other trophic guilds, and (2) we used Mantel tests to test if the extend of change in α-diversity ($\Delta\alpha$) in one trophic guild among plots correlates with the change in other trophic guilds at the subplot ($\Delta\alpha$ between pairs of subplots averaged within plots) or plot (total α within plot) level. Therefore, Manhattan distance matrices were calculated for each trophic guild at plot level ($N = 35$).

Beta-diversity was calculated using Bray–Curtis distances between either all pairs of subplots or plots based on species abundances using the function *bcdist* within the ecodist package for R (Goslee and Urban, 2010). At subplot level we (1) correlated the mean Bray–Curtis distance between subplots between trophic guilds using plot as the unit of replication (Pearson's product moment correlation, $N = 35$) and (2) we correlated Manhattan distance matrices based on mean Bray–Curtis distances between all pairs of subplots between trophic guilds using plot as the unit of replication (Mantel tests, $N = 35$). For β-diversity at the plot-level, Bray–Curtis distances between all pairs of plots were calculated. Correlations between the distance matrices of pairs of trophic guilds were then tested using Mantel tests ($N = 35$).

All Mantel tests (Legendre and Legendre, 1998; Mantel, 1967) were based on Monte-Carlo simulations with 9999 permutations. 95% confidence limits of Mantels R were calculated using a bootstrapping procedure with 9999 iterations based on resampling without replacement. To correct for multiple testing we used Bonferroni corrections in all correlation analyses.

3. Results

In total we found 149 plant species, 80 herbivores (2083 individuals), 81 xylophages (853), 206 predators (1828), 107 mycetophages (1956), and 52 detritivores (1715, divided into 12 coprophages (64), 22 necrophages (1480), and 18 saprophages (170) species). Detritivores were excluded from further analyses due to low sample size; in 66% of all traps fewer than three individuals were found (in 30% of all traps zero individuals), only in 12% of all traps more than ten individuals occurred. For more details on the abundance and diversity of the different trophic guilds see the Supplementary S4. A complete list of sampled species including their trophic classification is given in S7.

3.1. Diversity partitioning

In general, β-diversity made up a large proportion of overall diversity (Fig. 1a), in accordance to hypothesis H1. Alpha-diversity at the subplot level was generally lower than expected from a random distribution of individuals while β-diversity at the plot level was generally higher than expected (Figs. 1b and S5-2). Among-forest class β-diversity showed generally the lowest deviation from a random distribution of individuals. Even though overall deviations from random distributions were more pronounced when abundant species were weighed more strongly (especially for $q = 2$) results were very similar independent of the value of q choses (Figs. 1 and S5-2). One remarkable exception was the lowest β-diversity level (subplot). At $q = 2$, β-diversity of herbivores, xylophages and predators was lower and those of plants higher than expected from a random distribution of individuals, whereas at $q = 0$, β-diversity of xylophages, predators and mycetophages was greater than expected by chance.

While the relative contribution of spatial diversity scales to total gamma diversity as well as the deviations from random distributions at particular spatial scales differed among trophic guilds, it was not generally more similar between more closely connected trophic guilds, in contrast to our hypothesis H2 (Fig. 1). Plants and mycetophages showed contrasting patterns. For α-diversity, plants showed the highest, mycetophages the lowest negative deviation from a random distribution. For β-diversity, the spatial level deviating most from expectation differed among the trophic guilds: for plants it was the among-plot level while for mycetophages it was the regional level. For herbivores and predators both the among-plot and among-region spatial levels contributed most to overall β-diversity. Finally, for xylophages, the among-plot, among-forest class and among-region level showed similar deviations from expectations.

Beta-diversity partitioning into the two separate components of spatial turnover and nestedness revealed that overall spatial turnover accounted for between 84% and 96% of total β-diversity (Figs. 2 and S5-2). This suggests that bias caused by differences in species richness between plots is negligible.

3.2. Correlations of diversities among trophic guilds

In contrast to our hypothesis H3, α-diversity as well as $\Delta\alpha$ was not generally more strongly correlated between plants and herbivores or herbivores and predators than among other pairs of trophic guilds. At the subplot as well as at the plot level, α-diversity or $\Delta\alpha$ of herbivores correlated positively with the α-diversity or $\Delta\alpha$ of predators and α-diversity or $\Delta\alpha$ of xylophages with α-diversity or $\Delta\alpha$ of mycetophages (Table 1, Fig. 3, Table S6-1; at the plot level marginally not significant after Bonferroni-correction). No significant correlation between plants and herbivores was observed, neither at subplot nor at the plot level.

The same was true for correlations of β-diversity among trophic guilds at the subplot and plot level. Average β-diversity among subplots was neither significantly correlated between plants and any of the consumer trophic guilds nor among consumer guilds (Table 2, Fig. 3, Table S6-2). At the among-plot level, β-diversity was highly significantly correlated among consumer feeding guilds (Fig. 3). The correlation between β-diversity of plant species and β-diversity of predators and mycetophages was much stronger than between plants and herbivores (Figs. 3 and S6-1).

4. Discussion

Our study is one of the first that analyzed spatial diversity patterns across a variety of trophic guilds within only one dominating
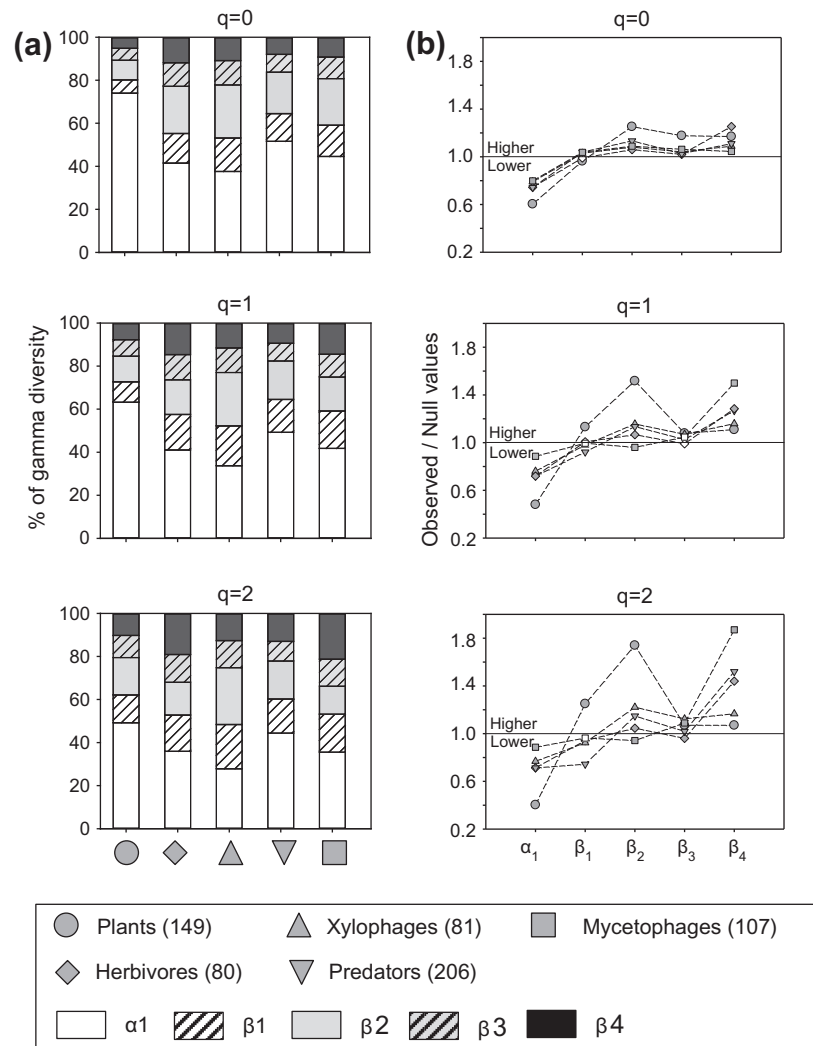
Fig. 1. Multiplicative diversity partitioning (without sample weighting) of species of different trophic guilds including plants (using 3 of 7 randomly selected subplots per experimental plot) and beetles (Coleoptera) using Whittaker's multiplicative formula. (a) The contribution of different α- and β-components of diversity to total gamma diversity at five spatial scales: subplot (α_1, β_1), plot (β_2), forest class (β_3), and region (β_4). Forest classes refer to differences in structure, measured as mean total gap fraction per plot (see Figure S2-1). (b) The deviation from a Null distribution is illustrated by dividing observed values by the mean of Null values for each trophic guild. Results of q-statistics are shown for three q-values with increasing weighting of abundant species from 0 to 1 to 2. The total number of sampled species is given in brackets. Significant differences at the 0.05 level between diversity estimates and null estimates using 10,000 unrestricted individual-based randomizations are indicated by gray, non-significant differences by white symbols. The pattern was very similar to those observed when all seven subplots per plot of the plant survey were considered (Fig.S5-2 of the Supplementary S5).

vegetation type (i.e. European beech-dominated forests) of high conservation relevance. Our first main result is that β-diversity at all spatial levels considered contributed significantly to total diversity. At almost all spatial scales and all trophic guilds considered β-diversity was higher than expected from a random distribution of individuals whereas α-diversity was lower than expected by chance. Moreover, β-diversity patterns were much stronger correlated among trophic guilds than α-diversity. This emphasizes the need to consider β-diversity at all spatial levels including smaller spatial scales in conservation strategies. A second main result of our study is that β-diversity was largely due to spatial turnover rather than nestedness indicating that assemblages in species-poor plots are not a subset of assemblages of species-rich plots. Our third main result is that similarities among trophic guilds in the partitioning of total diversity were not as hypothesized: while plants and herbivores, or herbivores and predators, are connected through direct feeding links, only herbivores and predators were partly more similar than the average of the pairs of groups. This

could be shown in terms of diversity partitioning and correlations of α- and β-diversity.

Below we will explore possible mechanisms underlying these results and derive recommendations for future conservation strategies.

The use of different values of the q-metric (Jost, 2007) varies the importance of dominant species. Results of the partitioning analyses were surprisingly similar for different values of q, i.e. different weightings of abundant species, with notable exceptions. At almost all trophic guilds, and independent of the abundance weighting, α-diversity was generally significantly lower than expected from a random distribution of individuals, i.e. there were more individuals locally than expected and individuals of a species thus tended to be locally aggregated. Such local concentrations of individuals of the same species have been frequently observed in diversity partitioning studies (Müller and Gossner, 2010; Summerville et al., 2006; Veech et al., 2003). Several mechanisms can lead to such aggregation such as a small-scale clumped distribution of
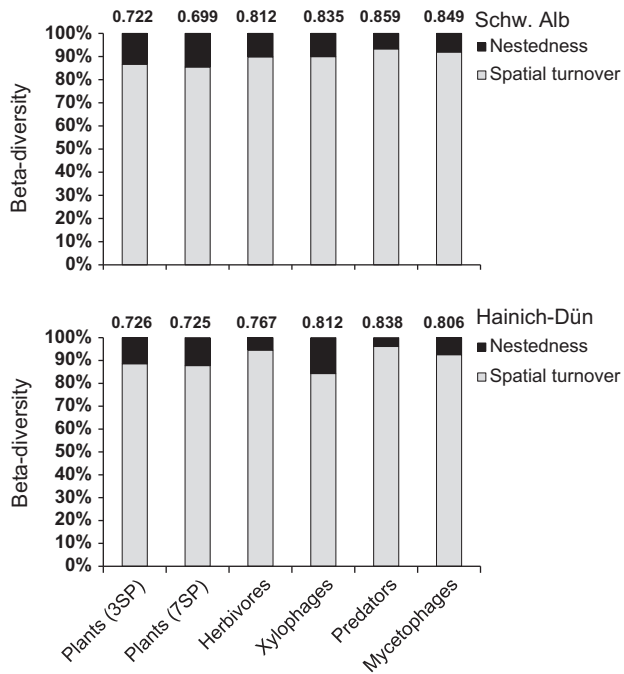
Fig. 2. Additive partitioning of beta-diversity (multiple-site dissimilarities) into turnover (measured as Simpson dissimilarity) and nestedness (measured as nestedness-resultant fraction of Sorensen dissimilarity) components. The sum of both values is given on top of each bar.

resources or local dispersal limitation. Our study emphasizes that this is a general phenomenon across all guilds and taxonomic levels investigated.

For β-diversity, results differed between the different spatial scales investigated. At the lowest spatial level, among subplots, species turnover was often not significantly different from a random distribution of individuals, and significant deviations from the random distribution could be higher or lower than expected. When β-diversity was mainly based on abundant species ($q = 2$), β-diversity was less than expected for herbivores, xylophages and predators, and higher than expected for plants. In contrast, when all species were weighted equally ($q = 0$) which corresponds to a stronger influence of rare species, β-diversity was greater than expected for xylophages, predators and for mycetophages. This suggests that rare beetles show a heterogeneous distribution within plots, probably because of a clumped distribution of their resources, i.e. dead wood amount and quality. In plants, within microhabitat variability might determine the small scale distribution of abundant plant species. At the highest spatial levels, among

regions, β-diversity was higher than expected from a random distribution of individuals, for all trophic guilds, and independent of the species abundance weighting, reflecting different species pools in the two regions. Finally, for the intermediate spatial levels, among forest classes and among plots, results were quite varied. Species turnover was particularly high among forest classes in plants, when all species were weighted equally. For xylophages, predators and mycetophages patterns were similar independent of abundance weighting. Among plots, species turnover within forest classes was higher than expected by a random distribution of individuals, for all trophic guilds (mycetophages only for $q = 0$). This may indicate high within-forest class variability of important habitat factors for the different trophic guilds and especially for plants which showed the highest deviation from a random distribution at this scale. One interpretation is that characterizing forests by "stand openness" ignores other, possibly more important structuring variables for the plant and animal communities. For example forest management might affect the distribution of dead wood resources for xylophages (Meyer and Schmidt, 2011) and site history might be crucial for plants (Wulf, 2003). These factors are not necessarily correlated to stand openness.

The similarity in the overall patterns, such as the general high contribution of β-diversity to total γ-diversity with β-diversity being significantly higher than expected by chance at most spatial scales, independent of the particular value of q used suggests that spatial diversity patterns mainly result from a change in species composition rather than from variation in species abundances which is in line with results of other large-scale diversity studies (Devictor et al., 2010; Gossner and Müller, 2011). This indicates that a pre-selection of priority sites for conservation regarding β-diversity could focus on dominant species, which are easier to assess. In order to maintain high species diversity at smaller scales rarity and trophic guilds need to be considered because of the relative high importance of smaller scales, i.e. among-subplot and among-plot level, in rare species and high variability among trophic guilds. For example, at subplot-level β-diversity of mycetophagous, xylophagous and predacious species and at plot level of mycetophagous species was only higher than expected from a random distribution at $q = 0$ (see also Gossner and Müller, 2011).

Generally, α-diversity showed largely independent pattern in different trophic guilds, with significant correlations observed only between herbivores and predators and between xylophages and mycetophages. Beta-diversity above subplot level, however, was highly correlated between most trophic guilds. Other studies investigating patterns of α- and β-diversity across taxa arrived at different conclusions. In line with our results Kessler et al. (2009) suggest that β-diversity patterns might be generally more congruent across taxa and trophic guilds, based on their studies on

Table 1
Correlations (Pearson's product moment correlation) among trophic guilds in Simpson α-diversity at the (a) subplot (df = 103) and (b) plot level (df = 33). Bold: significant correlations after correcting for multiple testing (Bonferroni correction; $p < 0.005$).

|	Herbivores		Xylophages		Predators		Mycetophages	
	t-Value	p-Value	t-Value	p-Value	t-Value	p-Value	t-Value	p-Value
(a)								
Plants (3 subplots)	1.904	0.060	0.364	0.176	2.364	0.020	2.445	0.016
Herbivores			1.856	0.066	**4.071**	**<0.001**	**3.143**	**0.002**
Xylophages					1.902	0.060	**4.607**	**<0.001**
Predators							2.441	0.016
(b)								
Plants (7 subplots)	−0.191	0.850	−0.077	0.939	0.040	0.968	−0.240	0.812
Plants (3 subplots)	1.221	0.231	0.410	0.685	0.799	0.430	0.059	0.954
Herbivores			0.999	0.325	**3.280**	**0.002**	−0.564	0.576
Xylophages					−0.294	0.771	2.022	0.051
Predators							−0.126	0.900
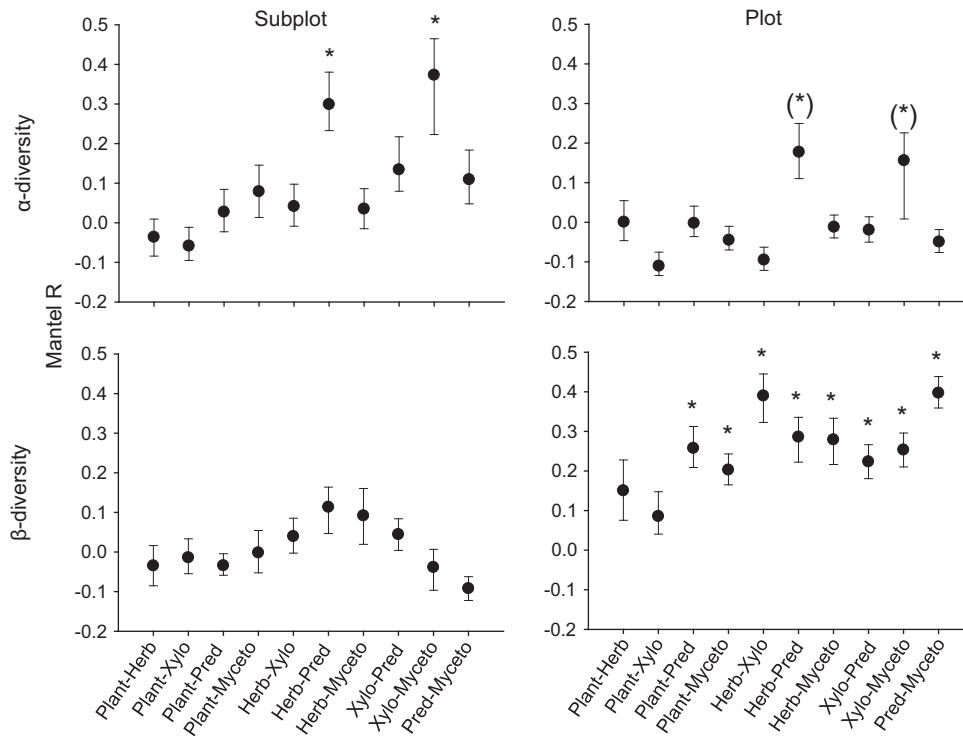
Fig. 3. Correlation between Δα- (reciprocal Simpson) and β-diversity (Bray–Curtis distances) of different trophic guilds at subplot (mean Δα among subplots per plot) and plot level based on a Mantel test (simulated by Monte-Carlo technique based on 9999 permutations, *N* = 35). In subplot level analyses Δα- and β-diversity among subplots was averaged at the level of plots. Three of seven randomly selected subplots of the plant survey are considered. Confidence limits are calculated based on a bootstrapping with 9999 iterations. The main results were similar to that observed by considering all seven subplots of the plant survey (as example see Fig. S6-1 of the Supplementary S6). *Significant and (*) marginally not significant after correcting for multiple testing (Bonferroni correction; *p* < 0.005).

Table 2
Correlation among trophic guilds of β-diversity among subplots (Bray–Curtis distance between pairs of subplots), averaged at the level of plots (Pearson's product moment correlation, df = 33; Bonferroni correction for multiple testing: significant at *p* < 0.005).

	Herbivores		Xylophages		Predators		Mycetophages	
	t-Value	*p*-Value	*t*-Value	*p*-Value	*t*-Value	*p*-Value	*t*-Value	*p*-Value
Plants (7 subplots)	−0.928	0.360	−1.768	0.086	−1.041	0.305	−1.561	0.128
Plants (3 subplots)	−1.398	0.172	−1.348	0.187	−1.028	0.978	−1.850	0.073
Herbivores			1.235	0.226	0.324	0.748	2.081	0.045
Xylophages					−0.271	0.788	0.982	0.333
Predators							0.365	0.712

different taxa in rainforest and agroforestry sites in Indonesia. In contrast, Cabra-Garcia et al. (2012) found cross-taxa β-diversity correlations to be lower than cross-taxa α-diversity, by investigating diversity patterns of five groups of litter invertebrates in different vegetation types in Colombia. This suggests that the transferability of results among different ecosystems might be limited and the possibility of deducing taxa that might work as surrogate for one another is strongly restricted. Mandl et al. (2010) showed in a study of 28 locations in three regions in Ecuador that even plant taxa (i.e. ferns, mosses, liverworts and lichens) that share commonalities in ecology and reproductive biology, do not share universal patterns for α- or β-diversity. Overall, on average only 5% (±31% SD) of the variance in species richness of one taxonomic group could be predicted by species richness of other groups. For European beech forests we found Mantel *R*-values of 0.2–0.4 for β-diversity correlations between beetle trophic guilds at plot level. This indicates that, in contrast to α-diversity, β-diversity among insect trophic guilds might be well correlated in this ecosystem. Further studies including a wide range of other taxa and trophic guilds are needed to test for generalizability.

In contrast to our hypothesis H3, correlations of α-diversity or β-diversity between more strongly connected trophic guilds were not higher than between less strongly connected ones. We observed a significant correlation of α-diversity between herbivores and predators and between xylophages and mycetophages, but not between any two of the other levels in the forest understorey and not regarding β-diversity at the subplot level. This suggests that the drivers of α-diversity in general, and species turnover at the subplot level in particular vary among different trophic guilds, although in some cases α-diversity might be driven by bi-trophic interaction (e.g. herbivores-predators) or similar resource requirements (possibly dead wood in xylophages and mycetophages).

Specialization in herbivores on a small number of plant species caused by coevolutionary processes is a widely known phenomenon (Schoonhoven et al., 1995). Hence a strong dependency between species diversity and community composition of plants and herbivorous insects can be expected. Jabot and Bascompte (2012) presented a modeling approach to analyze the effects of bitrophic interactions, e.g. plant–herbivore interactions, and network structure on patterns of α- and β-diversity in metacommunities. One of their major results was that bitrophic interactions were

likely to decrease α-diversity and increase β-diversity, for both plant and animals. Thus, high levels of β-diversity as found in our study, are consistent with the prediction of networks of bitrophic interactions among the species. True interactions between species cannot be deduced from trap-samples alone and need to be tested by appropriate methodology. However, the weak correlation found between diversities of plants and herbivores in our study indicates that different factors are crucial in these trophic levels.

5. Conclusions

Our results clearly emphasizes the high importance of different β-diversity scales, in particular those among forest plots and regions, for overall diversity. The highly congruent diversity partitioning among rare and abundant species and among trophic guilds and the high correlation of β-diversity above subplot level between the latter indicates that this is a more general phenomenon. Our study further indicates that this applies not only for contrasting habitat types (e.g. forest and agricultural sites), but also for a single one, such as beech-dominated forests. Exceptions to the general pattern such as contrasting patterns of different guilds at smaller spatial scales and the observed independence of α-diversity among trophic guilds, however, indicate more complex multi-trophic interactions and therefore call for caution in conservation planning. Three important implications for conservation can be deduced from our results: (1) heterogeneity of beech forests at different spatial scales should be supported in conservation strategies to enhance biodiversity and related functions; (2) the high spatial turnover suggests that conservation efforts should be concentrated on a large number of not necessarily the richest sites and this is also supported by studies on genetic diversity (Rauch and Bar-Yam, 2004); (3) while a pre-selection of priority sites for conservation at large spatial scale might be justified by a low number of trophic guilds and more abundant species, at smaller scale recommendation for conservation strategies based on single taxa or trophic guild is difficult because of the varied response of the species in our study.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.06.033.

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