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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