

Divergent responses of β -diversity among organism groups to a strong environmental gradient

MICAEL JONSSON,^{1,†} TORD SNÄLL,² JOHAN ASPLUND,³ KARINA E. CLEMMENSEN,⁴ ANDERS DAHLBERG,⁴
BRIGHT B. KUMORDZI,⁵ BJÖRN D. LINDAHL,⁶ JARI OKSANEN,⁷ AND DAVID A. WARDLE⁵

¹Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

²Swedish Species Information Centre, Swedish University of Agricultural Sciences, Box 7007, SE-750 07 Uppsala, Sweden

³Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Aas, Norway

⁴Department of Forest Mycology and Plant Pathology, Uppsala BioCenter, Swedish University of Agricultural Sciences, Box 7026, SE-750 07 Uppsala, Sweden

⁵Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden

⁶Department of Soil and Environment, Swedish University of Agricultural Sciences, Box 7014, SE-75007 Uppsala, Sweden

⁷Department of Ecology, University of Oulu, FI-90014 Oulu, Finland

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Abstract. A limited understanding of how variation in the species composition among communities (i.e., β -diversity) changes along natural environmental gradients, and the mechanisms responsible, inhibits our ability to understand large-scale biodiversity change resulting from either natural or anthropogenic drivers. Therefore, our aim was to test key drivers of β -diversity patterns along a strong, natural environmental gradient for seven widely different organisms groups, that is, root-associated fungi, litter fungi, soil nematodes, vascular plants, epiphytic lichens, beetles, and spiders. Using previously published community-level data from boreal-forested islands, we calculated α -diversity and β -diversity for each of the seven organism groups. Out of several available environmental variables, we identified four variables, that is, ecosystem age, total C storage, net primary productivity (NPP), and N-to-P ratio, as potential predictors of variation in β -diversity. We found that ecosystem age was the variable with the highest overall importance. We then used two different methods to quantify the relative importance of stochastic and deterministic processes underlying patterns in β -diversity along the ecosystem age gradient, and our detailed knowledge based on prior data collection in the study system to mechanistically explain among-group differences in these patterns. We found divergent responses in β -diversity along the age gradient for the seven different organism groups, due to among-group differences in the relative importance of deterministic vs. stochastic community assembly, and attributed these results to reliance on resources from different energy channels that are not always related to NPP. Our results highlight the necessity to consider the importance of taxon-specific resources, and not only NPP, to obtain an understanding of β -diversity patterns among organism groups and ecosystems, as well as large-scale patterns in biodiversity. They therefore also suggest that management and protection of β -biodiversity in the landscape requires explicit consideration of a wide range of habitats.

Key words: beetles; biodiversity; deterministic processes; fungi; lichens; nematodes; spiders; stochastic processes; vascular plants.

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† **E-mail:** micael.jonsson@umu.se

INTRODUCTION

The often observed positive relationship between large-scale biodiversity and net primary productivity (NPP) is believed to be due to increasing variation in the species composition among communities (i.e., higher β -diversity) with increasing productivity (Chase and Leibold 2002, Harrison et al. 2006, Evans et al. 2008, Chase 2010). Theory states that such observed changes in β -diversity across NPP gradients can be mechanistically explained by relative changes in underlying deterministic and stochastic processes. Deterministic processes can result in predictable patterns in β -diversity along productivity gradients, because factors that vary along such gradients operate as filters that favor some species over others (Keddy 1992). For example, low NPP can filter against generalist species, resulting in a homogenization of communities (i.e., low β -diversity) among low-productive sites when compared to among high-productive sites (Székely and Langenheder 2014), although nutrient-enriched ecosystems may show the opposite pattern (Passy and Blanchet 2007, Donohue et al. 2009). Conversely, when NPP is not a limiting factor, stochastic processes may lead to higher species variation in the species composition among communities and random (unpredictable) patterns in β -diversity, because chance events such as random colonization or extinction are more important (Chase 2003). However, some theoretical models favor either purely stochastic (Hubbell 2001) or deterministic (Clark 2009) processes in driving variation in the species composition among communities, while empirical studies suggest that both processes are important (Chase 2010, Vellend et al. 2014). Hence, the relative role of these processes as drivers of β -diversity continues to be debated (Chase and Meyers 2011, Rosindell et al. 2011, Vellend et al. 2014).

Understanding patterns in biodiversity along environmental gradients has been at the core of ecological research for at least a century (Clements 1916, Gleason 1927, Fukami et al. 2005, Vellend 2010). Besides satisfying theoretical curiosity, insights into drivers of biodiversity patterns allow us to predict ecosystem responses to environmental change, and thereby enable more successful biodiversity protection, restoration,

and management (Palmer et al. 1997, Magurran 2015). However, while patterns in, and drivers of, local diversity (i.e., α -diversity) along environmental gradients are well studied and reasonably well understood (Gaston 2000), empirical studies on variation in the species composition among natural communities (i.e., β -diversity) are fewer (Condit et al. 2002, but see e.g., Zemunik et al. 2016) and most have focused on a single organism group or trophic level (e.g., Hubbell 2001, Condit et al. 2002, but see e.g., Soininen et al. 2007, Norfolk et al. 2015). Given that β -diversity is an important component of large-scale biodiversity, a more thorough understanding of whether, how, and why β -diversity of different groups of organisms varies along natural environmental gradients is necessary for a general understanding of biodiversity and, thus, more successful protection and management of overall biodiversity (Magurran 2015).

Here, we used community-level data for seven different organism groups along a strong, natural, and well-characterized environmental gradient (Wardle et al. 1997, 2003, 2012a), to identify environmental drivers of β -diversity and investigate to which extent it is formed by stochastic (Hubbell 2001, Rosindell et al. 2011) vs. deterministic (Clark 2009) processes. Further, we test whether β -diversity of different organism groups, occupying different habitats and trophic positions, responds in similar ways to environmental drivers (*sensu* Chase 2010). The strong environmental gradient, along which the data were collected, involves a series of 30 pristine, boreal-forested islands in two adjacent lakes in northern Sweden.

We used this study system to investigate the impact of key environmental conditions on α -diversity (i.e., species richness per unit area within islands) and β -diversity (i.e., variation in the species composition of assemblages among islands), as well as processes determining β -diversity, using previously published community data for seven different organism groups, specifically root-associated fungi (Clemmensen et al. 2015), saprophytic litter fungi (Clemmensen et al. 2015), soil nematodes (Jonsson et al. 2009), vascular plants (Kumordzi et al. 2015a), epiphytic lichens (Asplund et al. 2014), beetles (Jonsson et al. 2009), and spiders (Jonsson et al. 2009). In our analyses, we used two measures of α -diversity, that is,

species richness and “effective number of species” (Jost 2007), and two measures of β -diversity, that is, the Jaccard index and the Bray–Curtis dissimilarity index. The extent of background data collected from this study system (e.g., Wardle et al. 1997, 2003, 2012a, b, Hyodo and Wardle 2009, Jonsson and Wardle 2009, Jonsson et al. 2009, Clemmensen et al. 2015, Kumordzi et al. 2015a, b) provides the opportunity to generate plausible and well-supported explanations for observed results.

METHODS

Study system

The study system consists of 30 pristine, boreal-forested islands, which show no signs of human impact (e.g., forestry or nutrient enrichment; Wardle et al. 1997, 2012a, b), in lakes Uddjaure and Hornavan in northern Sweden (65°55' N to 66°09' N; 17°43' E to 17°55' E). The islands differ in size, and therefore disturbance frequency by wildfire (Wardle et al. 1997, 2003), with large islands getting struck by lightning more often than small islands. Large islands have therefore on average burnt more recently (Wardle et al. 1997, 2003), resulting in that the islands collectively form a 5350-year chronosequence of time since the most recent fire. Studies along long-term chronosequences of this type enable insights about drivers of biodiversity over large spatio-temporal scales that are not possible with other approaches (Walker et al. 2010, Zemunik et al. 2016). In this study system, as islands become smaller and time since last major fire (i.e., ecosystem age) increases, available soil nutrients, rates of decomposition processes, plant standing biomass, and NPP decline, whereas total C storage (due to sequestration in the soil) and soil N-to-P ratio increase (Wardle et al. 1997, 2003, 2012a; Appendix S1: Table S1). Further, the vascular plant community changes along the gradient, with Scots pine (*Pinus sylvestris*) and bilberry (*Vaccinium myrtillus*) dominating on large islands, birch (*Betula pubescens*) and lingonberry (*Vaccinium vitis-idaea*) dominating on mid-sized islands, and Norway spruce (*Picea abies*) and crowberry (*Empetrum hermaphroditum*) dominating on small islands (Appendix S1: Table S1). As island size declines and time since fire increases, there is a greater level of coexistence of plant

species, and thereby an increased species richness (α -diversity) of several groups of organisms (Jonsson et al. 2009, Wardle et al. 2012a). Further, previous tests have revealed that there is no evidence of island area per se impacting plant and animal communities except through determining fire regime (Jonsson et al. 2009, 2011, Wardle et al. 2012a).

The islands also differ in isolation, with respect to neighboring islands, and in distances to nearest mainland (0.3–3.3 km), but this isolation is not correlated to island size, or any of the key environmental drivers of plant and animal diversity (Jonsson et al. 2009, Asplund et al. 2014). Further, the low level of isolation among these islands does not have any measurable influences on the community structure of the studied organism groups, relative to effects of ecosystem age (i.e., island area; Jonsson et al. 2009, Asplund et al. 2014). Results from more than 20 years of extensive prior data collection from this study system (e.g., Wardle et al. 1997, 2003, 2012a, b, Jonsson et al. 2009, Clemmensen et al. 2015, Kumordzi et al. 2015a, b) have revealed no evidence of other potentially confounding factors, than the ones primarily investigated, that vary along the gradient in such a way as to influence interpretations (Vellend 2010).

Collection of community data

We utilized community-level (both presence–absence and relative abundance) data for each of seven groups of organisms collected from all 30 islands constituting the chronosequence, that is, root-associated fungi, litter fungi, soil nematodes, vascular plants, epiphytic lichens, beetles, and spiders. For each group, sampling was conducted on all islands within a two-week period in the summer (July and/or August) in fixed-area plots using commonly used and established methods. The actual area sampled differed among organism groups reflecting differences in organism size and abundance, in line with conventional practice for each group. Detailed descriptions of the methods used for collecting community data of the seven organism groups are presented in the original publications reporting this data (Jonsson et al. 2009, Asplund et al. 2014, Clemmensen et al. 2015, Kumordzi et al. 2015a); brief descriptions are as follows. Community data for spiders, beetles, and nematodes were

collected over two consecutive years; spiders and beetles were collected in pitfall traps (250 mL, $n = 10$ per island), while extraction of humus cores (each 25 mm in diameter, 10 cm deep; $n = 30$ per island) was used to obtain nematodes (Jonsson et al. 2009). Epiphytic lichen community composition on trunks of *Betula pubescens* trees was recorded by establishing 16 grids on each island, that is, four grids on each of four trees (Asplund et al. 2014). The four grids on each tree were placed 0.2 and 1.3 m above the ground level on both the north- and south-facing sides. Each grid was 28 × 8 cm with 100 intersection points, and each lichen species at each intersection point was recorded (Asplund et al. 2014). Vascular plant community composition was determined by recording all plants present in a 10 m radius plot on each island (Kumordzi et al. 2015a) and estimating biomass of each species from allometric equations based on size characteristics (foliar density for understory species; diameter for trees; Wardle et al. 2003, 2012b). Litter and root fungal community composition was determined in humus cores (3 cm in diameter, 20 cm deep; $n = 8$ per island) by 454 pyrosequencing of amplified fungal ITS2 markers (litter communities based on 400 reads, root communities based on 800 reads per island; Clemmensen et al. 2015). Plots were always located at similar distances from the shore regardless of island size, to minimize the possibility of edge and microclimatic effects confounding the results (Wardle et al. 1997, 2003).

Measures of α -diversity and β -diversity

We calculated α -diversity (i.e., local, within-island species diversity) and β -diversity (i.e., variation in the species composition among islands) for each of the seven organism groups for the 30 islands. We used two measures of β -diversity: one ignoring local abundances on islands (the Jaccard index) while the other accounting for local abundances (the Bray–Curtis dissimilarity index). We also used two α -diversity measures, that is, species richness and the “effective number of species” (Jost 2007).

Environmental variables

Out of several environmental variables measured on each island for previous publications from this system (Wardle et al. 1997, 2003, 2012b),

we identified four as potential predictors of variation in β -diversity, that is, ecosystem age (^{14}C date), total C storage, NPP, and N:P ratio. Detailed descriptions of methods for measuring these variables are given in the original publications reporting the data that we used (i.e., Wardle et al. 1997, 2003, 2012b), and brief descriptions of these methods can be found in Appendix S1. Out of these variables, we selected ecosystem age and NPP a priori as primary environmental variables, as these have previously been shown to influence β -diversity, and because theoretical reasons have been proposed as to why they should have an effect (Chase and Leibold 2002, Fukami et al. 2005, Chase 2010). Further, because there is also an interest in how diversity relates to C sequestration (Luyssaert et al. 2008) and N:P ratio (Fujita et al. 2014), we designated these variables a priori as having secondary importance.

Statistical analyses

We started by sequentially testing the ability of each of the four selected environmental variables to explain the β -diversity (Bray–Curtis dissimilarity index and Jaccard index) among the islands of each organism group, using permutational multivariate analysis of variance. While the quality of this analysis depends on whether all relevant environmental variables are measured and included in the model or not, extensive prior data collection from this study system (Wardle et al. 1997, 2003, 2012b, Jonsson et al. 2009, Asplund et al. 2014, Clemmensen et al. 2015, Kumordzi et al. 2015a, b) has identified the selected environmental variables as those that are the most important drivers of community composition among the studied organism groups. *F* testing based on sequential sums of squares from 999 permutations of the raw data (i.e., species × site matrix) was used to identify which environmental variable was of primary importance for explaining variation in β -diversity, and what other variables explained additional variation. Following our a priori assignments of variables as primary or secondary, we performed sequential tests on all combinations of either ecosystem age or NPP in first or second order, and either total C storage or N:P ratio in third or fourth order. In six of seven cases, we found ecosystem age to be of primary importance for explaining variation in β -diversity; in

Table 1. Sequential tests of relationships between predictor variables and β -diversity (Bray–Curtis dissimilarity index and Jaccard index).

Organism group	Predictor variables				Deterministic processes (%)	Stochastic processes (%)
	Ecosystem age (yr)	NPP (kg·m ⁻² ·yr ⁻¹)	Total C storage (kg/m ²)	Soil N:P ratio		
Bray–Curtis						
Spiders	0.002	0.155	0.639	0.236	9.6	90.4
Nematodes	0.023	0.047	0.360	0.426	15.1	84.9
Beetles	0.009	0.415	0.464	0.525	10.7	89.3
Epiphytic lichens	0.013	0.123	0.269	0.141	9.8	90.2
Vascular plants	0.034	0.386	0.815	0.305	11.9	88.1
Litter fungi	0.003	0.203	0.063	0.150	6.6	93.4
Root fungi	0.033	0.007	0.099	0.517	10.9	89.1
Jaccard						
Spiders	0.004	0.256	0.655	0.180	7.0	93.0
Nematodes	0.044	0.024	0.311	0.397	13.1	86.9
Beetles	0.011	0.420	0.627	0.393	8.3	91.7
Epiphytic lichens	0.036	0.174	0.302	0.187	6.7	93.3
Vascular plants	0.025	0.459	0.704	0.149	10.4	89.6
Litter fungi	0.004	0.236	0.070	0.157	5.4	94.6
Root fungi	0.029	0.005	0.094	0.484	9.2	90.8

Notes: NPP, net primary productivity. Values of P and total explained (deterministic) and unexplained (stochastic) variances are shown. Significant relationships ($P < 0.05$) are presented in bold.

one case, NPP was slightly more important (Table 1). Total C storage and N:P ratio always had low explanatory power. Hence, in subsequent analyses we chose ecosystem age as the single predictor variable of β -diversity.

We then used two different analytical methods (i.e., measures) to quantify the relative importance of stochastic and deterministic processes underlying patterns in β -diversity, based on the variance explained by the key environmental variable (i.e., ecosystem age). Null model analysis is recommended for testing patterns in β -diversity (Chase 2010, Anderson et al. 2011, Chase et al. 2011). We therefore tested whether the observed relationships of β -diversity with ecosystem age differed from the relationships for communities constructed by three randomly generated null models (999 permutations), which is the first way in which we quantify the relative importance of stochastic processes for driving patterns in β -diversity. To do this, we divided the island systems into three ecosystem age classes, that is, young, mid-aged, and old (based on ¹⁴C measurements of ecosystem age), with $n = 10$ per class. First, we randomized species abundances among islands (c0_samp; Oksanen et al. 2014). This shuffles abundances (and α -diversity) among islands, but retains γ -diversity and

total species abundance. Second, we randomized species abundances among species within islands (swsh_samp_c; Oksanen et al. 2014). This retains α -diversity, γ -diversity, and total species abundance. Third, we applied binary null models (i.e., ignoring species abundance), shuffling species presence on each island, but retaining α -diversity and species frequencies (quasiswap; Oksanen et al. 2014). We illustrate β -diversity among ecosystem age groups as distance to the centroid within each group (Anderson 2001), and present the highest (i.e., most conservative) P -values obtained from using the quantitative null models.

As a complement to the observed changes in β -diversity along the ecosystem age gradient (Fig. 1a–g), we also investigated the relative role of stochastic and deterministic processes in shaping community structure through time based on standard effect size (SES; Chase 2010), and this is the second way in which we quantify the relative importance of stochastic processes for driving patterns in β -diversity. Specifically, we investigated whether variation in distance from the centroid within each ecosystem age group was higher or lower than given by the three null model communities described above (Oksanen et al. 2014). Positive SES values indicate community

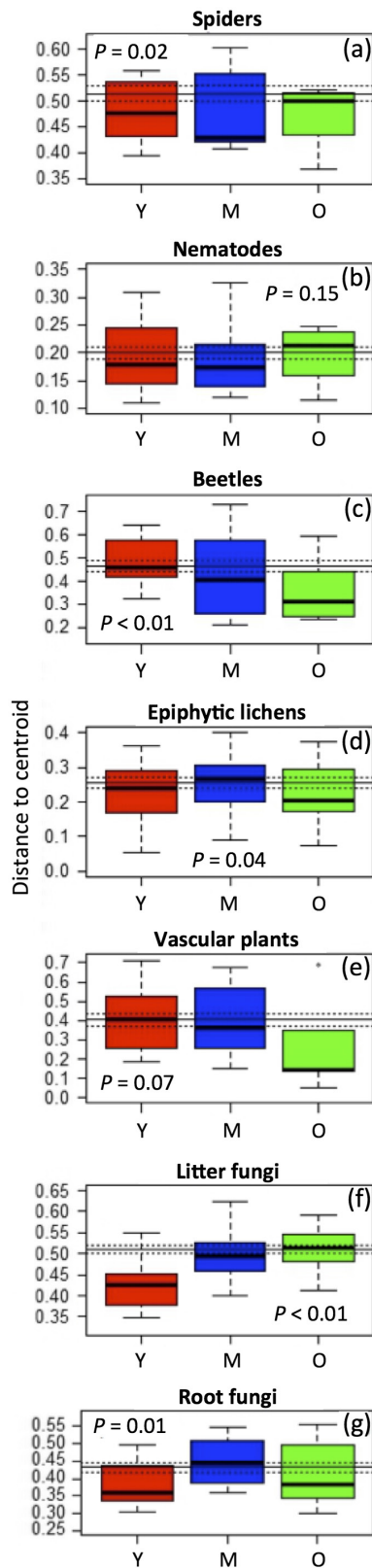


Fig. 1. Patterns in β -diversity (Bray–Curtis dissimilarity, distance to centroid) along an ecosystem age gradient, for spiders (a), nematodes (b), beetles (c), epiphytic lichens (d), vascular plants (e), litter fungi (f), and root fungi (g). Y, young (red); M, mid-aged (blue); and O, old (green) ecosystems. P-values are for tests of deviation in β -diversity among ecosystem age classes compared with overall β -diversity simulated by null models (Table 2). Horizontal lines show mean diversity and dashed lines ± 1 SE.

divergence (i.e., higher β -diversity than expected) under the null model, due to increased relative importance of stochastic processes. Negative values indicate community convergence (i.e., lower β -diversity than expected) due to increased relative importance of deterministic processes.

We also tested whether α -diversity of each organism group was explained by the same four environmental variables as for β -diversity, with generalized linear models, using the order of variables listed above. Species richness was assumed to follow an overdispersed Poisson distribution, while the effective number of species (Jost 2007) was assumed to follow a normal distribution. Model deviance explained (R^2) and whether or not each covariate explained a significant amount of variation in α -diversity in the sequential tests were reported.

Finally, we explored community composition among ecosystem age groups using ordination plots based on nonmetric multidimensional scaling. Each point on the plot reflects the community composition of an island in multidimensional space and the distance between points reflects difference in community composition among islands according to the Bray–Curtis dissimilarity index. Thus, smaller distances and therefore occupation of a smaller ordination space by islands within a group indicate higher similarity in community composition (i.e., community convergence) among islands when compared to a group of islands occupying a larger ordination space. Subsequently, we tested statistically whether the community composition of any of the ecosystem age groups was more homogenous than the composition among all islands. This was done for each ecosystem age group by joining the points on the plot by lines to construct minimum convex hulls, and testing

whether the area of any of the group-specific hulls was smaller than random joining of points into three groups. Values of P based on 999 permutations were reported. All statistical analyses were conducted using R (R Core Team 2012) and the vegan library (Oksanen et al. 2014).

RESULTS

For all organism groups, the variation in β -diversity among islands was best explained by the difference in ecosystem age and thus by relative position along the chronosequence, with the exception of root fungi where NPP was slightly more important (Table 1). The effect of ecosystem age was always statistically significant for both quantitative (i.e., Bray–Curtis dissimilarity index) and binary (i.e., Jaccard index) measures of β -diversity. Besides for root fungi, there was also an additional effect of NPP for nematodes, but total C storage and N:P ratio did not explain significant amounts of the variation in β -diversity for any of the organism groups. The ways in which β -diversity responded to ecosystem age differed greatly among organism groups (Fig. 1a–g), that is, significantly hump-shaped patterns for lichens and root fungi, significantly U-shaped pattern for spiders, significantly negative for beetles, and significantly positive for litter fungi. In contrast, α -diversity showed broadly similar, increasing responses to ecosystem age (Fig. 2a–g); it increased significantly with age for four of seven organism groups when species richness was used, although using effective number of species this pattern was only noted for two groups (Appendix S1: Table S2).

Among organism groups, the majority of variation in β -diversity remained unexplained, while the predictor variables explained between 6.6% and 15.1% of total variation in β -diversity among groups (Bray–Curtis dissimilarity; Table 1). Using ecosystem age as the single predictor variable, this relatively weak influence of what can be presumed to be deterministic processes was still enough to cause quantitative β -diversity to be significantly different from what would be expected if community assembly was purely stochastic, that is, when compared to null models, for five of the seven organism groups (Fig. 1a–g; for results on binary β -diversity, Table 2). The analyses used to determine

Table 2. Values of P for tests of deviation in β -diversity (Bray–Curtis dissimilarity) among the ecosystem age classes compared with null model community composition.

Organism group	quasiswap	c0_samp	swsh_samp_c
Spiders	0.47	<0.01	0.02
Nematodes	0.13	0.15	0.14
Beetles	0.30	<0.01	<0.01
Epiphytic lichens	0.20	0.04	0.03
Vascular plants	0.51	0.06	0.07
Litter fungi	<0.01	<0.01	<0.01
Root fungi	<0.01	0.01	0.01

Notes: As null models, quasiswap (binary) shuffles species presence on each island, but retains α -diversity, c0_samp (quantitative) shuffles abundances (and α -diversity) among islands, but retains γ -diversity and total species abundance, and swsh_samp_c (quantitative) randomizes species abundances among species within islands, but retains α -diversity, γ -diversity, and total species abundance. Values of P in bold are significant at $P = 0.05$.

the relative importance of stochastic and deterministic processes, that is, involving calculations of SESs within ecosystem age classes and plots of two-dimensional (ordination) spaces for comparisons among ecosystem age classes, confirmed that the different β -diversity patterns observed among organism groups resulted from differences in how the relative importance of deterministic and stochastic processes shifted with ecosystem age (Figs. 3 and 4). For spiders, deterministic processes had a significant effect for mid-aged ecosystems (Fig. 3a), resulting in lower β -diversity at this stage (Fig. 1a). Further, for root fungi, the SESs indicated a high relative importance of deterministic processes (i.e., community convergence) in both mid-aged and old ecosystems (Fig. 3g), but these results did not corroborate the higher β -diversity (i.e., community divergence) in mid-aged ecosystems (Fig. 1g). However, for both litter and root fungi, the significantly smaller ordination space (i.e., community convergence) in young ecosystems followed by community divergence in mid-aged ecosystem (Fig. 4f, g) confirmed the observed patterns in β -diversity (Fig. 1f, g). Similarly, although the SESs did not indicate that the decrease in beetle β -diversity with ecosystem age (Fig. 1c) was due to deterministic processes (Fig. 3c), the occurrence of community convergence in mid-aged ecosystems (i.e., significantly smaller ordination space; Fig. 4c) shows that

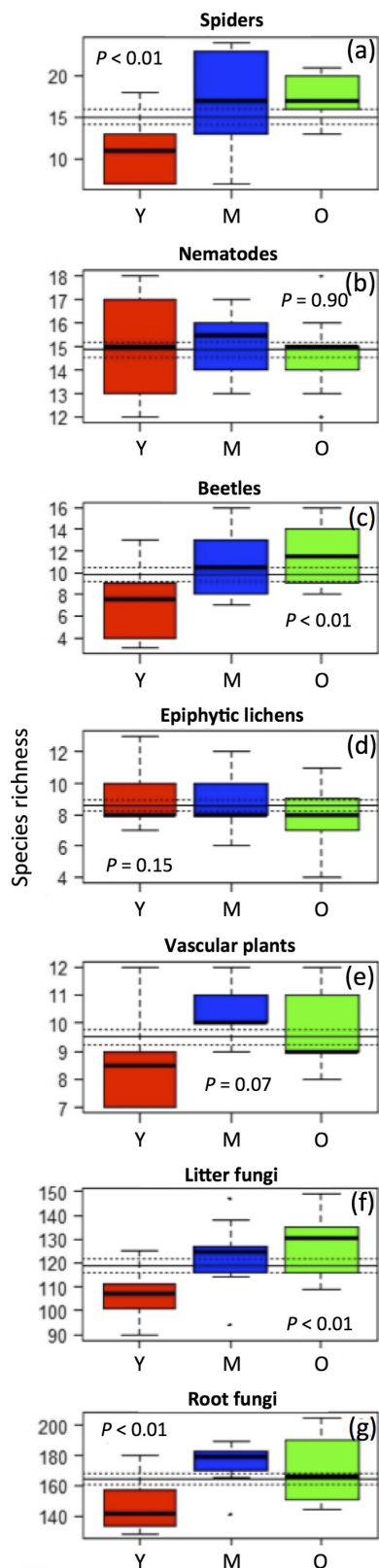


Fig. 2. Patterns in α -diversity (species richness) along an ecosystem age gradient, for spiders (a), nematodes (b), beetles (c), epiphytic lichens (d), vascular plants (e), litter fungi (f), and root fungi (g). Y, young (red); M, mid-aged (blue); and O, old (green) ecosystems. P -values are for tests of relationships between α -diversity and ecosystem age. Horizontal lines show mean diversity and dashed lines ± 1 SE.

deterministic processes are significant in shaping beetle β -diversity at that stage of ecosystem development.

DISCUSSION

The observed nonrandom changes in β -diversity along the ecosystem age gradient serve as evidence for shifts in the relative importance of deterministic and stochastic processes (Chase 2010), given that a β -diversity that is lower than expected from random assembly is indicative of a greater relative importance of deterministic processes. Thus, while some theories predict that purely stochastic processes are responsible for patterns in β -diversity (Hubbell 2001, Rosindell et al. 2011), we found that deterministic processes also had an impact. The observed divergent responses in β -diversity to the ecosystem age gradient among different groups of organisms, despite broadly similar responses in α -diversity, are in line with previous studies showing that diversity measured at different spatial scales, such as α -diversity and β -diversity, may show contrasting responses to the same environmental drivers (Chase and Leibold 2002). However, in contrast to previously proposed uniform responses in β -diversity to changed environmental conditions (Fukami et al. 2005, Chase 2010), the divergent responses in β -diversity among organism groups are indicative of taxon-specific drivers of β -diversity (cf. Soininen et al. 2007). For example, the decreasing beetle β -diversity with ecosystem age (Fig. 1c) is evidence of an increasingly more deterministic community assembly, while increasing litter fungi β -diversity (Fig. 1f) is the result of stochastic community assembly becoming more prevalent with ecosystem age.

Given that changes in environmental drivers with ecosystem age are well characterized in this

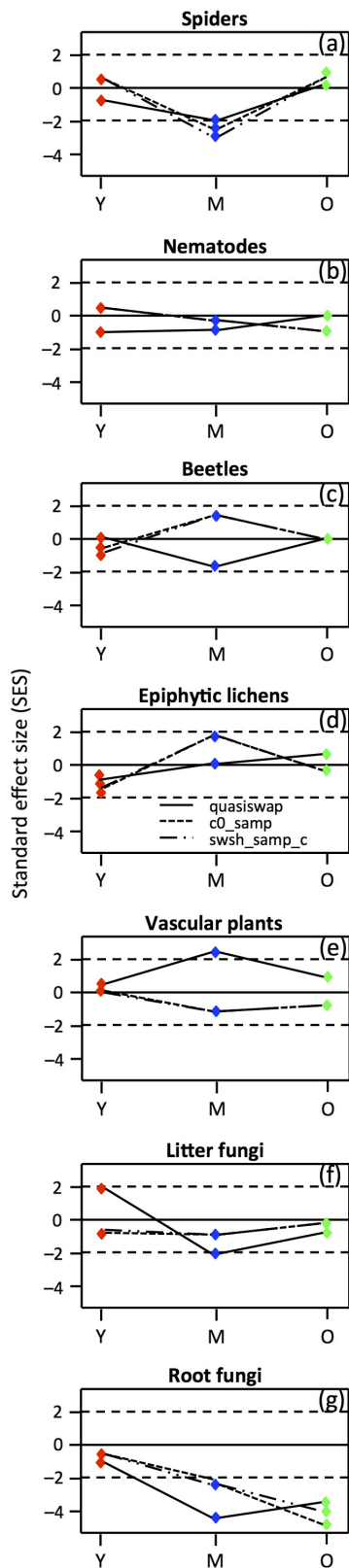


Fig. 3. Standard effect sizes (SESs) for seven different organism groups along an ecosystem age gradient, for spiders (a), nematodes (b), beetles (c), epiphytic lichens (d), vascular plants (e), litter fungi (f), and root fungi (g). Three null models are used, that is, the binary “quasiswap” (full line), and the quantitative “c0_samp” (dashed line) and “swsh_samp_c” (dotted line). As null models, quasiswap (binary) shuffles species presence on each island, but retains α -diversity, c0_samp (quantitative) shuffles abundances (and α -diversity) among islands, but retains γ -diversity and total species abundance, and swsh_samp_c (quantitative) randomizes species abundances among species within islands, but retains α -diversity, γ -diversity, and total species abundance. Y, young (red); M, mid-aged (blue); and O, old (green) ecosystems. Dashed horizontal lines denote 95% confidence limits.

study system (e.g., Wardle et al. 1997, 2003, 2004, 2012a, b; Appendix S1: Table S1), we are able to suggest specific explanations as to why the relative importance of deterministic processes, and thus β -diversity, varies along the gradient and among organism groups. Because β -diversity has been shown to increase along natural gradients in ecosystem productivity (Chase and Leibold 2002, Harrison et al. 2006, Chase 2010), and because our study system shows a decline in NPP with increasing ecosystem age (Wardle et al. 1997, 2003, 2004), our a priori expectation was that β -diversity would decrease with ecosystem age. While we found this to be true for beetles, and marginally significantly so for vascular plants (Fig. 1e), the other organism groups showed nonexisting, nonlinear, or even increasing patterns in β -diversity (cf. Zemanik et al. 2016).

For beetles, which were mainly herbivorous or predaceous, the decline in β -diversity with increasing ecosystem age is most likely due to declining abundance of terrestrial food sources, in the form of not only plants but also invertebrate prey. Increasingly limiting terrestrial food resources may act as an environmental filter against generalist species (Székely and Langenheder 2014), resulting in significant community convergence (Figs. 1c and 4c). Similarly, for spiders, increasingly limiting terrestrial food resources result in community convergence in

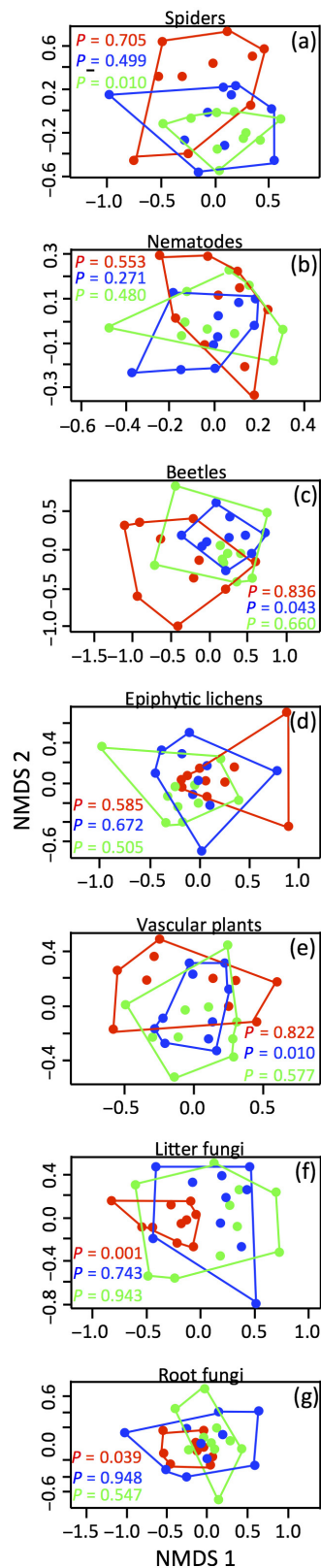


Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination plots of community composition in two-dimensional space, for spiders (a), nematodes (b), beetles (c), epiphytic lichens (d), vascular plants (e), litter fungi (f), and root fungi (g). Each point reflects the community composition of an ecosystem in multidimensional space and the distance between them reflects differences in community composition (Bray–Curtis dissimilarity). Lines represent the minimum convex hulls around the community data of each ecosystem. Red, young; blue, mid-aged; and green, old ecosystems. P -values refer to tests of whether the variation in community composition of any of the ecosystem age group-specific hulls is different from a hull embracing all points.

the transition from young to mid-aged ecosystems (Figs. 1a and 3a). The lack of further convergence in old ecosystems (i.e., small islands) can be explained by spiders utilizing NPP sourced from surrounding lake water in the form of emergent aquatic insects; this resource has previously been shown to subsidize spiders most on small islands (Hyodo and Wardle 2009, Jonsson and Wardle 2009). Likewise, rather than responding to terrestrial NPP, the pattern in epiphytic lichen β -diversity (Fig. 1d) tracks the abundance of their substrate (birch tree trunks), which peaks in mid-aged ecosystems (Wardle et al. 1997, Asplund et al. 2014; Appendix S1: Table S1).

In our study system, plant litter and root heterogeneity increases with ecosystem age despite NPP decreasing, as a consequence of increased vascular plant species richness and build-up of the litter layer (Wardle et al. 1997, 2012a, Kumordzi et al. 2015a; Appendix S1: Table S1). Hence, the significant community convergence in young ecosystems for both litter and root fungi (Fig. 4f, g) and divergence in mid-aged ecosystem (Fig. 1g, h) correspond to lower resource heterogeneity (acting as an environmental filter) in young ecosystems and increased resource heterogeneity with ecosystem age. The community convergence in root (but not litter) fungi in the oldest, relative to mid-aged, ecosystems (Figs. 1g and 3g) can be explained by root fungi being more directly linked to aboveground terrestrial NPP (Table 1; Clemmensen et al. 2015). As such, our results show that fungal

β -diversity primarily is shaped by heterogeneity in resources (Astorga et al. 2014), which in this system increases with decreasing terrestrial NPP (Wardle et al. 1997, Kumordzi et al. 2015a), rather than terrestrial NPP per se (Martínez-García et al. 2015), but that a very low level of terrestrial NPP may still cause community convergence (Zemunik et al. 2016).

CONCLUSIONS

While some theory proposes uniform responses of β -diversity to environmental factors such as successional age (Fukami et al. 2005) and NPP (Chase 2010), we found widely divergent responses in β -diversity among organism groups (cf. Soininen et al. 2007). We propose that these divergent responses in β -diversity are due to different organism groups using resources from taxon-specific energy channels. As such, these results are relevant to biodiversity management that has traditionally focused on a limited number of environmental conditions (primarily NPP) and on the conservation of α -diversity. However, conservation of β -diversity is crucial for maintaining biodiversity at larger spatial scales (Gaston 2000). Further, as our results show, β -diversity is maximized in distinct types of ecosystems for different major groups of organisms, and conservation to maximize β -diversity would therefore require focus on a range of ecosystem types in the landscape, not just those that maximize α -diversity. More generally, we emphasize that understanding of both types of diversity, and their responses to extrinsic environmental factors for different groups of organisms, is important for better predicting the outcomes of conservation efforts, as well as how large-scale biodiversity responds to human impacts including those associated with global change.

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