

# A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems

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## Abstract

**Aim:** The number of studies investigating the nestedness and turnover components of beta diversity has increased substantially, but our general understanding of the drivers of turnover and nestedness remains elusive. Here, we examined the effects of species traits, spatial extent, latitude and ecosystem type on the nestedness and turnover components of beta diversity.

**Location:** Global.

**Time period:** 1968–2017.

**Major taxa studied:** From bacteria to mammals.

**Methods:** From the 99 studies that partition total beta diversity into its turnover and nestedness components, we assembled 269 and 259 data points for the pairwise and multiple site beta-diversity metrics, respectively. Our data covered a broad variation in species dispersal type, body size and trophic position. The data were from freshwater, marine and terrestrial realms, and encompassed geographical areas from the tropics to near polar regions. We used linear modelling as a meta-regression tool to analyse the data.

**Results:** Pairwise turnover, multiple site turnover and total beta diversity all decreased significantly with latitude. In contrast, multiple site nestedness showed a positive relationship with latitude. Beta-diversity components did not generally differ among the realms. The turnover component and total beta diversity increased with spatial extent, whereas nestedness was scale invariant for pairwise metrics. Multiple site beta-diversity components did not vary with spatial extent. Surprisingly, passively dispersed organisms had lower turnover and total beta diversity than flying organisms. Body size showed a relatively weak relationship with beta diversity but had important interactions with trophic position, thus also affecting beta diversity via interactive effects. Producers had significantly higher average pairwise turnover and total beta diversity than carnivores.

**Main conclusions:** The present results provide evidence that species turnover, being consistently the larger component of total beta diversity, and nestedness are related to the latitude of the study area and intrinsic organismal features. We showed that two beta-diversity components had generally opposing patterns with regard to latitude. We highlight that beta-diversity partition may give additional insights into the underlying causes of spatial variability in biotic communities compared with total beta diversity alone.

## KEYWORDS

biodiversity, body size, dispersal, global, macroecology, meta-analysis, nestedness, turnover

## 1 | INTRODUCTION

Biodiversity is heterogeneously distributed across the Earth. Variation of biological communities across space or time (i.e., beta diversity) has therefore attracted increasing attention (Alahuhta et al., 2017; Anderson et al., 2011; Koleff, Gaston, & Lennon, 2003; König, Weigelt, & Kreft, 2017; Nekola & White, 1999; Soininen, Lennon, & Hillebrand, 2007; Soininen, McDonald, & Hillebrand, 2007; Tuomisto 2010a, 2010b; Viana et al., 2016). Beta diversity interacts with alpha-diversity gradients, and both of these biodiversity components result from community assembly through local and regional filters. Thus, beta diversity may capture the dynamic nature of biodiversity patterns better than simple measures of alpha diversity alone. Recently, beta diversity has also been considered as an essential metric to inform patterns in regional biodiversity and contribute to conservation planning (Socolar, Gilroy, Kunin, & Edwards, 2016). Such information about spatial variation in beta diversity is thus also prerequisite for testing general ecological theories (Baselga, 2010) and guiding practical management decisions (Socolar et al., 2016).

Publications about beta diversity range from original papers or case studies (Gianuca, Declerck, Lemmens, & De Meester, 2017; Hill, Heino, Thornhill, Ryves, & Wood, in press; Hortal et al., 2011) to meta-reviews searching for general patterns in beta diversity (Soininen, Lennon et al., 2007; Soininen, McDonald et al., 2007) and methodological or conceptual papers discussing different approaches to quantify beta diversity (Anderson et al., 2011; Baselga, 2010; Carvalho, Cardoso, & Gomes, 2012; Jurasinski, Retzer, & Beierkuhnlein, 2009; Koleff et al., 2003; Tuomisto, 2010a, 2010b). However, at the heart of discussion about beta diversity are its two components, namely turnover and nestedness. The former refers to beta diversity attributable to species replacement, whereas the latter indicates species loss or gain, that is, richness differences between the samples (Baselga, 2010). In nature, species turnover may reflect species sorting by the environment or dispersal processes, whereas nestedness is often related to ordered

extinction-colonization dynamics (Si, Baselga, Leprieur, Song, & Ding, 2016).

Baselga (2010) was the first to propose a general framework for the partition of total beta diversity ( $\beta_{\text{total}}$ ) into the turnover ( $\beta_{\text{turnover}}$ ) and nestedness components ( $\beta_{\text{nestedness}}$ ). Despite receiving some criticism (Carvalho et al., 2012; Chen & Schmera, 2015), Baselga's (2010) approach has been successfully implemented to account for climatic (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; Hortal et al., 2011; Tisseuil, Leprieur, Grenouillet, Vrac, & Lek, 2012), environmental (Alahuhta et al., 2017), spatial (Hill et al., in press; Viana et al., 2016) or temporal effects on biological communities (Angeler, 2013; Baeten et al., 2012), and it remains one of the most important methodological frameworks for beta-diversity analyses. The novelty of the approach lies in the fact that it enables deeper insights to be gained into beta diversity, possibly revealing causal mechanisms driving the variation in biodiversity. Clearly, in most studies using beta-diversity partitioning, the dominant component has been turnover, suggesting that a difference in richness often plays a smaller role in generating beta-diversity patterns (Hill et al., in press; Tisseuil et al., 2012; Viana et al., 2016). This is a typical finding across a set of local communities, whereas biogeographical studies focusing on large-scale assemblages also often find a considerable nestedness component (Baselga, 2010).

Even if species turnover may dominate in various ecosystems and taxonomic groups, we would expect that the magnitudes of turnover and nestedness components show predictable variation among different biological, ecological and geographical settings. We first hypothesized ( $H_1$ ) that total beta diversity and turnover would decrease with latitude because both beta-diversity meta-analyses (Soininen, Lennon et al., 2007) and comprehensive case studies (Qian, 2009; Qian, Badgley, & Fox, 2009) suggest that species turnover decreases with increasing latitude (Table 1). This is because species turnover may reflect the direct effects of physical limiting factors or ecological and evolutionary processes, which are also influenced by latitude (Qian et al., 2009). However, we expected that nestedness might in turn

**TABLE 1** Summary of the hypotheses and the main results

Hypothesis	Turnover	Nestedness	Key references
H <sub>1</sub> : Latitude	Decreases with latitude ( <i>supported</i> )	Increases with latitude ( <i>supported</i> )	Baselga (2010); Baselga et al. (2012); Qian (2009); Soininen, Lennon et al. (2007)
H <sub>2</sub> : Realm	Lowest in marine ecosystems ( <i>not supported</i> )	Lowest in marine ecosystems ( <i>supported</i> )	Clarke (1992); Hillebrand (2004)
H <sub>3</sub> : Study extent	Increases with study extent ( <i>supported</i> )	Increases with study extent ( <i>partly supported</i> )	Baselga (2010); Dobrovolski et al. (2012)
H <sub>4</sub> : Dispersal type	Highest for passively dispersed taxa ( <i>partly supported</i> )	Not specified	Soininen, Lennon et al. (2007)
H <sub>5</sub> : Body size	Scales positively with body size for passively dispersed taxa ( <i>not supported</i> ), but negatively for actively mobile taxa ( <i>supported</i> )	Scales positively with body size for passively dispersed taxa ( <i>supported</i> ), but negatively for actively mobile taxa ( <i>not supported</i> )	Finlay et al. (1996); Gaston and Blackburn (1996)
H <sub>6</sub> : Trophic position	Increases with trophic position in a food web ( <i>not supported</i> )	Increases with trophic position in a food web ( <i>not supported</i> )	Hillebrand (2004)

*Note.* The evaluation of results (*supported* or *not supported*) is based on the multiple linear model of pairwise or multiple site metrics. *Partly supported* means that hypothesis is correct according to the bivariate linear model, but not according to the multiple linear model.

increase toward poles owing to the higher number of local and regional extinctions related to lower productivity, historical factors and harsh environmental conditions near the poles (Baselga, 2010; Baselga, Gómez-Rodríguez, & Lobo, 2012; Castro-Insua, Gómez-Rodríguez, & Baselga, 2016; Dobrovolski et al., 2012). Second ( $H_2$ ), we hypothesized that beta diversity would show predictable variation among different realms. We expected that marine environments would show lower total beta diversity, turnover and nestedness compared with freshwater or terrestrial systems owing to the lesser environmental heterogeneity and greater connectivity among marine sites (Clarke, 1992; Hillebrand, 2004; Soininen, Lennon et al., 2007). Third ( $H_3$ ), we hypothesized that both turnover and nestedness would increase with spatial extent, possibly because of the stronger dispersal limitation and stronger environmental filtering owing to longer environmental gradients. In particular, nestedness would be highest at the largest extents (i.e., continental or global extents), as extinctions should be more evident only at very large geographical extents, generating gradients in alpha diversity (Baselga, 2010; Dobrovolski et al., 2012).

We further expected that species characteristics or traits reflecting the biology of individual organisms would also have a detectable effect on total beta diversity and its components. Given that beta diversity measures compositional differences between sites, one potential driver of such differences is the homogenizing effect of dispersal (Leibold et al., 2004). We thus hypothesized ( $H_4$ ) that passively dispersed taxa have higher  $\beta_{\text{total}}$  and especially  $\beta_{\text{turnover}}$  than active and mobile taxa on a general level (Soininen, Lennon et al., 2007). However, such an expected pattern is confounded by organisms' body sizes, because many passively dispersed taxa are small, even microscopic, and thus they probably have good dispersal ability (Finlay, 2002). Conversely, many large organisms are active and mobile, being able to fly (e.g., birds, bats and butterflies) or move on the ground (e.g., mammals, lizards and snakes). We therefore expect that body size might show a different influence on beta diversity depending on whether organisms are actively or passively dispersed. For passively dispersed taxa, we expected ( $H_{5a}$ ) that beta-diversity components would increase with body size (Finlay, Esteban, & Fenchel, 1996), whereas for actively dispersed (i.e., mobile and flying) taxa, beta-diversity components would decrease with body size ( $H_{5b}$ ). This is because for actively dispersed taxa, range sizes typically increase with body size (Gaston & Blackburn, 1996), and large, active species thus exhibit lower beta diversity. Collectively, we assumed that the general dispersal type–beta-diversity and body size–beta-diversity relationships are neither straightforward nor linear, and that dispersal type and body size would probably show interactive effects on beta diversity components (Soininen, McDonald, & Hillebrand, 2007). Finally ( $H_6$ ), we hypothesized that beta diversity would increase with organisms' trophic position in a food web, based on the observation that the assemblages of species at high trophic levels typically have steep spatial gradients in alpha diversity (Hillebrand, 2004). Therefore, we expected that nestedness, in particular, would increase with trophic position.

To the best of our knowledge, a quantitative synthesis over beta-diversity components across different organismal groups, geographical gradients or ecosystem types is still lacking. Here, we compiled a large

number of beta-diversity partition results for many different taxonomic assemblages from the literature and tested the ideas presented above. In addition, we ran beta-diversity partition analyses for various community data sets we collected by ourselves. These data cover a broad variation in major characteristics of organisms, such as body sizes, dispersal types and trophic positions, range from terrestrial to aquatic systems and encompass geographical areas from the tropics to near-polar regions.

## 2 | MATERIAL AND METHODS

In our meta-analysis, we included beta-diversity components both from (a) our own raw community data sets and (b) the results for beta diversity derived from various published sources. We report results using both average pairwise beta-diversity metrics and multiple site beta-diversity metrics. For thorough information about differences between the two approaches, see Baselga (2010) and Baselga (2013). Briefly, for estimating overall heterogeneity in communities, multiple site metrics may be more reliable than average pairwise metrics (Baselga, 2013).

First, we included the results from the papers that cite Baselga (2010) in the Web of Science. We decided to use the Baselga's (2010) approach here because it is the most widely used method to partition beta diversity. Moreover, the turnover component of the Podani family of metrics is correlated with richness difference, whereas the turnover component of the Baselga family of metrics is independent (Baselga & Leprieur, 2015). We included all papers that describe the study locations, study organisms and study extent and provide the values of beta-diversity components using the Baselga (2010) family metrics. We included both observational and experimental studies; however, only one study was experimental. For the comparison of partition methods, we ran analyses with the subset of data ( $n = 121$ ) using the Podani family (Podani & Schmera, 2011) average pairwise beta-diversity metrics. We found, however, that the turnover component of Podani and Schmera (2011) showed a very high correlation ( $r = .915$ ) with the Baselga (2010) metric, whereas nestedness and richness differences had clearly a lower correlation ( $r = .581$ ; Supporting Information Appendix S1).

Second, we assembled the community data from our own sources, data papers (e.g. Gibb et al. 2017) and *Ecological Archives*. [Correction added on 24 November 2017, after first online publication: The data source "Gibbs et al. 2017", was previously omitted and has been added to the earlier sentence and reference list.] We also searched for the raw data sets in the Dryad digital repository (<http://datadryad.org/>). We used the following search strings: community OR assemblage AND (a) mammals, (b) birds, (c) butterflies, (d) fish, (e) bats, (f) ants, (g) vascular plants, (h) bryophytes, (i) bees, (j) spiders, (k) snakes, (l) lizards, (m) trees, (n) amphibians, (o) insects and (p) marine. Some of the publications analysed were also obtained from the bibliographies of the papers that were screened. We calculated beta-diversity metrics using the betapart package (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017) in R version 3.2.2 (R Development Core Team, 2015). We standardized multiple site beta diversity using 15 sites.

We included only studies that address spatial taxonomic beta diversity. We thus excluded temporal studies and those focusing on functional or phylogenetic beta diversity. In total, we obtained 269

data points of average pairwise dissimilarities and 259 data points of multiple site dissimilarities. For a detailed list of studies ( $n = 99$ ) included, see data sources (Appendix – Data sources). Data will be available in Dryad once the paper is published.

Each estimate of  $\beta_{\text{turnover}}$ ,  $\beta_{\text{nestedness}}$  and  $\beta_{\text{total}}$  was classified with respect to three continuous variables (latitude, spatial extent and organism body size) and three categorical variables (organism dispersal mode, realm and trophic position). Organism body size was approximated as the  $\log_{10}$ -transformed wet mass (in grams) and derived for each organism group as an average from the literature (Hillebrand, 2004; Peters, 1983). Although the size range for organism group may be large (up to five orders of magnitude), it is small compared with the overall variation obtained across organism groups (12 orders of magnitude). However, we emphasize that the unknown variation in body masses within the organism group may generate residual variation in the data that could not be controlled. For more details on body size approximations, see Drakare, Lennon, and Hillebrand (2006) and Hillebrand (2004). Spatial extent was expressed as  $\log_{10}$ -transformed maximal linear distance (in kilometres) between the sampled sites. Organism dispersal mode was divided into the following four categories: mobile (e.g., fish and mammals), flying (e.g., birds and bats), passively dispersed (e.g., bacteria and protists) and organisms dispersed with seeds (i.e., gymnosperms and angiosperms). The variable realm was classified into freshwater, marine and terrestrial environments. Trophic position was categorized into autotrophs, herbivores, omnivores, decomposers and carnivores.

As a meta-regression approach, we used linear modelling (LM) to unite the effects of categorical and continuous variables on beta-diversity components and total beta diversity. We also ran the analyses with logit-transformed values of the response variables, but the results were highly similar compared with the untransformed values. Thus, we show here the results based on untransformed response variables for clarity. As the values of the response variables scale from zero to one, we also ran generalized linear models with beta distribution [GLM, betareg function in the package betareg (Zeileis et al., 2016) in R] to explain variation in beta diversity. However, as these models did not converge properly, possibly owing to the large number of categorical variables, we show here the results based on LM.

The continuous variables did not show strong inter-correlations (all  $r_p < .7$ ; Leathwick, Elith, & Hastie, 2006) and we thus incorporated all of them into the models. We also included an interaction term between trophic position and body size in the event that these interactions would be related to beta diversity. More information on the importance of interactions in meta-analyses can be found in Soininen, McDonald et al. (2007). For testing the hypothesis  $H_5$ , we ran simple bivariate correlations between beta-diversity metrics separately for passively and actively dispersed (i.e., mobile and flying) taxonomic groups.

We also ran models using the number of sampling sites (ranging between four and 296) as weights in order to put more emphasis on the data points [all data points for average pairwise metrics ( $n = 269$ ) and  $n = 249$  data points for multiple sites metrics] with larger sample sizes (Hadfield & Nakagawa, 2010). We calculated total heterogeneity in beta-diversity metrics using the weighted sums of squares, known as Q statistics (Hedges & Olkin, 1985).

We placed the most emphasis on the multiple linear model results rather than bivariate plots or boxplots, because linear regression describes the effects of variables in a multivariate model setting. It should be noted that even if some variable has a non-significant effect on a dependent variable when subjected to univariate analysis, it may still be a significant variable in a multivariate model setting when accounting for the covariance with other factors (Hillebrand, Frost, & Liess, 2008).

### 3 | RESULTS

The mean value for average pairwise  $\beta_{\text{turnover}}$  ( $n = 269$ ) was 0.530 ( $SD = 0.184$ , minimum = 0.114, maximum = 0.953), which was 5.7 times larger than that for average pairwise  $\beta_{\text{nestedness}}$  (mean = 0.093,  $SD = 0.054$ , minimum = 0.007, maximum = 0.320). The mean for average pairwise  $\beta_{\text{total}}$  was 0.623 ( $SD = 0.165$ , minimum = 0.140, maximum = 0.961). For multiple site metrics ( $n = 259$ ),  $\beta_{\text{turnover}}$  was likewise much larger than  $\beta_{\text{nestedness}}$ . The  $\beta_{\text{turnover}}$  and  $\beta_{\text{nestedness}}$  were negatively correlated ( $r = -.49$  and  $r = -.77$  for pairwise and multiple metrics, respectively). The  $\beta_{\text{total}}$  and  $\beta_{\text{turnover}}$  showed a highly positive correlation ( $r = .96$  and  $r = .90$ ), whereas  $\beta_{\text{nestedness}}$  had a weak negative correlation with  $\beta_{\text{total}}$  ( $r = -.22$  and  $r = -.41$ ). The total heterogeneity ( $Q_{\text{tot}}$ ) in beta-diversity metrics indicated significant ( $p < .001$ ) structure in the effect sizes except for nestedness (pairwise metrics:  $\beta_{\text{turnover}}$  482.6,  $\beta_{\text{nestedness}}$  32.0 and  $\beta_{\text{total}}$  360.8).

#### 3.1 | Spatial patterns and differences between ecosystems

Agreeing with our first hypothesis ( $H_1$ ), the pairwise  $\beta_{\text{turnover}}$ , the multiple site  $\beta_{\text{turnover}}$  and multiple site  $\beta_{\text{total}}$  all decreased significantly ( $p < .001$  for all, except  $p < .01$  for multiple site  $\beta_{\text{total}}$ ) with latitude (Table 2 and Figure 1; Supporting Information Appendices S2 and S3). In contrast, the multiple site  $\beta_{\text{nestedness}}$  showed a significant ( $p < .001$ ) positive relationship with latitude (Table 2; Supporting Information Appendix S3). A similar positive, albeit non-significant, latitudinal trend was found for the pairwise  $\beta_{\text{nestedness}}$ .

Our analysis did not generally confirm  $H_2$ , because the marine realm had lower beta diversity than the freshwater realm only for average pairwise  $\beta_{\text{nestedness}}$  in a multivariate model (Table 2).

Our analysis generally agreed with  $H_3$ , as  $\beta_{\text{turnover}}$  and  $\beta_{\text{total}}$  increased with spatial extent (Table 2 and Figure 1; Supporting Information Appendix S2). However, contrary to our hypothesis,  $\beta_{\text{nestedness}}$  was scale invariant. Multiple site metrics were not related to spatial extent.

#### 3.2 | Organismal variables

The degree of beta diversity was also related to some organismal variables as we expected. In  $H_4$ , we expected that beta diversity differs among organisms with different dispersal types. Contrary to our hypothesis, organisms that disperse passively had slightly lower  $\beta_{\text{turnover}}$  and  $\beta_{\text{total}}$  than flying organisms in a multivariate model

**TABLE 2** The detailed results of the linear models for explaining beta-diversity components using average pairwise ( $n = 269$ ) and multiple site metrics ( $n = 259$ )

Variable	Category or range	Pairwise turnover	Pairwise nestedness	Pairwise total	Multiple turnover	Multiple nestedness	Multiple total
Intercept		$0.40 \pm 0.18^*$	$0.16 \pm 0.06^{**}$	$0.56 \pm 0.16^{***}$	$0.79 \pm 0.13^{***}$	$0.04 \pm 0.07$	$0.83 \pm 0.10^{***}$
Log <sub>10</sub> body size (g)	−9.41 to 2.88	$0.01 \pm 0.01$	$0.01 \pm 0.00^*$	$0.01 \pm 0.01^*$	$-0.00 \pm 0.01$	$0.00 \pm 0.00$	$0.00 \pm 0.00$
Dispersal	Flying (47, 51)	0	0	0	0	0	0
	Mobile (39, 26)	$0.01 \pm 0.04$	$0.00 \pm 0.01$	$0.01 \pm 0.04$	$-0.03 \pm 0.04$	$0.05 \pm 0.02^{**}$	$0.01 \pm 0.03$
	Passive (172, 172)	$-0.17 \pm 0.07^*$	$0.03 \pm 0.02$	$-0.14 \pm 0.06^*$	$-0.08 \pm 0.06$	$0.07 \pm 0.03^*$	$-0.02 \pm 0.05$
	Seeds (11, 10)	$-0.40 \pm 0.10^{***}$	$0.02 \pm 0.03$	$-0.38 \pm 0.09^{***}$	$-0.07 \pm 0.08$	$0.08 \pm 0.04$	$0.00 \pm 0.06$
Trophic level	Carnivore (1, 1)	0	0	0	0	0	0
	Herbivore (18, 23)	$0.35 \pm 0.23$	$-0.11 \pm 0.07$	$0.24 \pm 0.20$	$0.13 \pm 0.17$	$-0.06 \pm 0.09$	$0.07 \pm 0.13$
	Omnivore (101, 80)	$0.15 \pm 0.16$	$-0.07 \pm 0.05$	$0.08 \pm 0.14$	$-0.01 \pm 0.12$	$-0.02 \pm 0.06$	$-0.04 \pm 0.09$
	Producer (99, 105)	$0.48 \pm 0.18^{**}$	$-0.08 \pm 0.06$	$0.40 \pm 0.16^*$	$0.21 \pm 0.14$	$-0.06 \pm 0.07$	$0.14 \pm 0.10$
	Decomposer (50, 50)	$2.29 \pm 0.41^{***}$	$-0.44 \pm 0.13^{**}$	$1.85 \pm 0.37^{***}$	$1.04 \pm 0.31^{**}$	$-0.47 \pm 0.16^{**}$	$0.57 \pm 0.23^*$
Realm	Freshwater (160, 173)	0	0	0	0	0	0
	Marine (16, 1)	$0.01 \pm 0.07$	$-0.06 \pm 0.02^*$	$-0.06 \pm 0.07$	$-0.00 \pm 0.12$	$0.01 \pm 0.06$	$0.01 \pm 0.09$
	Terrestrial (93, 85)	$-0.05 \pm 0.04$	$-0.01 \pm 0.01$	$-0.06 \pm 0.04$	$-0.06 \pm 0.03$	$0.05 \pm 0.02^{***}$	$-0.00 \pm 0.02$
Extent (km)	0.001–13,600	$0.02 \pm 0.01^*$	$0.01 \pm 0.00$	$0.02 \pm 0.01^{**}$	$-0.00 \pm 0.01$	$0.00 \pm 0.00$	$-0.00 \pm 0.00$
Latitude	0.7–70.0	$-0.01 \pm 0.00^{***}$	$0.00 \pm 0.00$	$-0.01 \pm 0.00^{***}$	$-0.01 \pm 0.00^{***}$	$0.01 \pm 0.00^{***}$	$-0.01 \pm 0.00^{**}$
Interaction terms	Decomposer $\times$ Body size	$0.19 \pm 0.04^{***}$	$-0.04 \pm 0.01^{**}$	$0.15 \pm 0.04^{***}$	$0.09 \pm 0.03^{**}$	$-0.04 \pm 0.02^*$	$0.05 \pm 0.023^*$
	Omnivore $\times$ Body size	$-0.04 \pm 0.01^{***}$	$-0.00 \pm 0.00$	$-0.05 \pm 0.01^{***}$	$-0.03 \pm 0.01^{***}$	$0.00 \pm 0.00$	$-0.03 \pm 0.01^{***}$
Adjusted $R^2$		0.308***	0.157***	0.300***	0.349***	0.266***	0.294***

Note. For each category, the number of data points are shown in parentheses for pairwise and multiple site metrics, respectively. For continuous variables, ranges are given. The regression parameter estimates for the categorical variables are measured as departures from the first class in each variable. Coefficient indicates how much beta diversity metric increases or decreases when the independent variable increases by one, when holding other independent variables constant. Standard errors are also shown for each estimate. \* $p < .05$ . \*\* $p < .01$ . \*\*\* $p < .001$ .

(Table 2). However, in bivariate linear models, passively dispersed organisms had significantly ( $p < .05$ ) higher  $\beta_{\text{turnover}}$  than flying taxa (Figure 1; Supporting Information Appendix S2). Organisms that disperse by seeds had significantly lower average pairwise  $\beta_{\text{turnover}}$  and pairwise  $\beta_{\text{total}}$  than flying organisms. The  $\beta_{\text{nestedness}}$  did not vary among different dispersal types.

On a general level, body size showed a relatively weak relationship with beta diversity. In multiple linear models, average pairwise  $\beta_{\text{nestedness}}$  and  $\beta_{\text{total}}$  increased with body size, whereas in a bivariate plot,  $\beta_{\text{total}}$  slightly decreased with body size (Table 2; Supporting Information Appendix S2). When passively dispersed taxa were analysed separately, average pairwise  $\beta_{\text{turnover}}$  scaled negatively, but non-significantly, with body size, thus disagreeing with our hypothesis  $H_{5a}$ . For mobile or flying taxa, average pairwise  $\beta_{\text{turnover}}$  scaled in a significantly ( $p < .05$ ) negative manner with body size, agreeing with  $H_{5b}$ . Average pairwise  $\beta_{\text{nestedness}}$  scaled in a significantly ( $p < .01$ ) positive manner with body size for passively dispersed taxa, agreeing with  $H_{5a}$ . For mobile or flying taxa,  $\beta_{\text{nestedness}}$  was not correlated with body size.

For trophic position, producers at the bottom of the food webs had significantly higher average pairwise  $\beta_{\text{turnover}}$  and  $\beta_{\text{total}}$  than carnivores with highest trophic position (Table 2). We note, however, that such a pattern was based only on small amounts of data, as carnivores were represented by one study only. Decomposers had significantly higher average pairwise  $\beta_{\text{turnover}}$  and  $\beta_{\text{total}}$ , but lower  $\beta_{\text{nestedness}}$  than

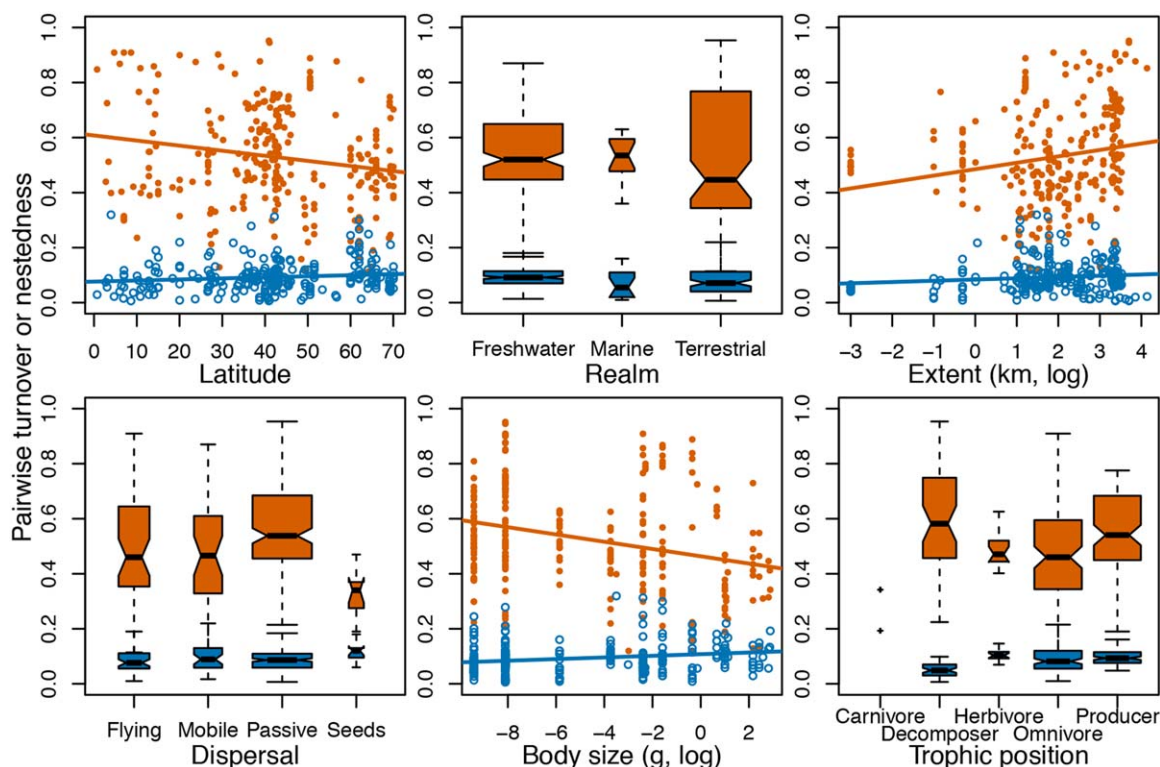
carnivores. Our hypothesis  $H_6$  about increasing beta diversity with increasing trophic position was therefore not clearly confirmed. Organisms with different trophic positions showed variable patterns along latitude, study extent and body size (Supporting Information Appendix S4). For example, only decomposers and producers had significant ( $p < .05$ ) latitudinal declines in  $\beta_{\text{turnover}}$ , and only  $\beta_{\text{nestedness}}$  of decomposers showed a significant positive relationship with latitude.

When multiple linear models were run using the number of sampling sites as a weight for each data point, the results largely agreed with unweighted analyses (Supporting Information Appendix S5). However, most patterns in weighted models were stronger, and these models had consistently higher explanatory power (adjusted  $R^2$ ) than unweighted models.

## 4 | DISCUSSION

Our analysis is the first quantitative synthesis about beta-diversity components across wide ranges of ecosystems, geographical regions and organismal groups. It allows the first step towards the more general view about the causes underlying turnover and nestedness. One of our new findings was that turnover is typically more than five times larger than nestedness (that in some data sets even approaches zero). Together with the finding that turnover correlates very strongly with total beta diversity (whereas nestedness does not), this suggests that





**FIGURE 1** Observed values ( $n = 269$ ) for the pairwise turnover (in brown, filled circles) and nestedness (in blue, open circles) component of beta diversity across latitude, realm, spatial extent, dispersal type, body size and trophic position. Significant ( $p < .05$ ) linear bivariate regression fits are also shown for latitude, extent and body size. Lines in boxes are medians, box ends are quartiles, whiskers show 95th percentiles, and circles show outliers. Widths of the boxes are proportional to the square roots of the number of data points in each category

turnover measures largely the same phenomenon as total beta diversity, that is, compositional dissimilarities of communities between sites, whereas nestedness may quantify more the bias introduced by richness differences between the sites. Second, we also documented that even if turnover and nestedness typically showed a negative correlation, they also responded independently to some of the predictor variables. Therefore, partition of beta diversity gives more insights into the factors driving spatial variability in biotic communities compared with a consideration of total beta diversity alone. For instance, this was evidenced by the opposing latitudinal patterns between the two beta-diversity components. Third, our analyses support the idea that the two beta-diversity components were related to both large- and local-scale variables, as latitude, realm and organismal features were correlated with the variation in the beta-diversity components. Next, we will discuss our findings with regard to our specific hypotheses.

#### 4.1 | Spatial patterns and differences between ecosystems

The results supported our first hypothesis about latitudinal patterns in beta diversity given that the total beta diversity and turnover decreased towards poles, whereas nestedness slightly increased with latitude. The former finding of a decreasing total beta diversity and turnover with latitude has been suggested by earlier meta-analyses of

beta diversity (Soininen, Lennon et al., 2007; Soininen, McDonald et al., 2007) and species–area relationships (Drakare et al., 2006), as well as large-scale terrestrial case studies (Qian, 2009; Qian et al., 2009). This finding suggests that species turnover among sites is higher in low latitudes, perhaps owing to either larger environmental heterogeneity or less efficient among-site dispersal, which are known to be among key drivers of species turnover (Leibold et al., 2004; Mouquet & Loreau, 2003). Such a latitudinal pattern in species turnover could also be related to a latitudinal cline in biotic interactions, often invoked to be stronger in low latitudes (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Willig, Kaufman, & Stevens, 2003). As competitive interactions, for example, take place locally rather than regionally, resulting in lower local richness, they are suggested to generate deeper latitudinal cline in regional than in local diversity (Hillebrand, 2004). As beta diversity measures the ratio between regional and mean local richness, this would lead to a latitudinal decline in beta diversity (Soininen, Lennon et al., 2007). What is more novel in the present analysis is that nestedness showed the opposite, that is, an increasing trend with increasing latitude. Such a pattern has been documented already by case studies for beetles (Baselga, 2010) and for amphibians, birds and mammals (Baselga et al., 2012; Dobrovolski et al., 2012) but, to the best of our knowledge, it has not previously been shown on a general level (i.e., across studies with a wide range of taxa). Although the pattern was weak, this finding suggests that ordered local or regional extinctions

and recolonizations might become slightly more common towards the poles, where environmental conditions are not favourable for most of the species and where conditions show higher variability in time compared with low-latitude environments. Moreover, the regions near the poles have been affected more by glaciation effects than regions at low latitudes, which may have slightly increased extinctions and recolonizations at high latitudes. Recently, Castro-Insua et al. (2016) documented a breakpoint for the beta diversity of terrestrial vertebrates at c. 30°, after which turnover decreased substantially, whereas nestedness increased. In our data, such a corresponding breakpoint occurred at 41° for turnover (Supporting Information Appendix S6). However, for nestedness, there was no such significant breakpoint in a regression fit. Collectively, these results show that such a breakpoint seems to be a general phenomenon for turnover.

We did not find clear evidence for our second hypothesis that marine ecosystems have overall lower beta diversity, but pairwise nestedness was nevertheless significantly lower in marine ecosystems than in freshwaters in a multivariate model. The lack of a clear distinction between marine and the other ecosystems in this respect disagrees with Soininen, Lennon et al. (2007), who documented the lowest beta diversity in marine systems, measured as the ratio between regional and local richness, and with Soininen, McDonald et al. (2007), who showed that spatial distance decay of community similarity is generally weaker in oceans than in the other realms. The reason for such a distinction between these studies is speculative at present, but may stem, at least in part, from methodological differences between these studies (i.e., how beta diversity is calculated) as well as overall a relatively low number ( $n = 16$  for pairwise metrics) of marine data points included in the present analysis. We emphasize, however, that not all previous meta-analyses have shown weaker diversity patterns in marine ecosystems than in freshwater or terrestrial ecosystems. For example, Drakare et al. (2006) documented larger slopes of species–area relationships for the marine realm than for freshwaters or most terrestrial ecosystems. Moreover, Hillebrand (2004) showed that marine and terrestrial taxa have steeper latitudinal alpha-diversity gradients than freshwater taxa. In sum, any generalizations about possible among-realm differences in terms of beta-diversity components are still somewhat premature until data allow an even more comprehensive analysis.

With regard to spatial scale, turnover and total beta diversity increased with study extent as we hypothesized, whereas nestedness did not vary with scale. We note, however, that such a finding was not very clear, as the present data set included relatively few smaller-scale studies and because multiple site beta-diversity metrics did not vary with scale. The finding that turnover slightly increased with study extent supports the idea that dispersal limitation and/or environmental filtering may increase with scale as a result of longer dispersal distances and environmental gradients, respectively (Heino et al., 2015). However, our analysis did not support the idea that nestedness would increase with extent, an expectation that was based on a reasoning that regional extinctions should be evident mostly at large spatial extents (Dobrovolski et al., 2012). This suggests that nestedness is most likely to be related to multiple factors, such as frequency of dispersal events, environmental heterogeneity and biotic interactions.

Such processes may be influential especially in data sets that cover smaller, metacommunity levels (Heino et al., 2015), typical for our collected data set, as many of our data points were derived from studies conducted at the scales ranging from 10 up to a few hundreds of kilometres. We believe that the relative influence of such processes may vary in space and time depending on the biological and ecological features of taxa (e.g., dispersal mode, body size and feeding habits) as well as on characteristics of the study system and region (e.g., dispersal barriers and ecosystem type). Therefore, although species turnover and total beta diversity seem to increase with spatial extent, as also documented earlier for small-scale beta diversity (Soininen, McDonald et al., 2007), we emphasize that nestedness may not vary with scale across studies as a result of complex colonization–extinction dynamics especially likely to occur within metacommunities (Heino et al., 2015). Nonetheless, it is likely that nestedness increases with latitude, for example, owing to glaciation-induced extinctions–recolonizations at large spatial extents when considered for a single taxonomic group only, as have been documented previously by Baselga (2010), Baselga et al. (2012) and Dobrovolski et al. (2012).

## 4.2 | Organismal variables

The turnover and nestedness patterns were also related to organism characteristics. Contrary to what was hypothesized, however, we first (a) found that passively dispersed taxa had lower turnover and total beta diversity in multivariate analyses than flying taxa. Second (b), for passively dispersed taxa, species turnover did not increase with body size as we hypothesized. These findings are counterintuitive at first glance and may be related to potential interactions between dispersal mode and body size because mobile taxa tend to be large bodied, whereas passively dispersed taxa were mostly micro-organisms or aquatic microcrustaceans in our data. This may be especially true because passively dispersed taxa had higher turnover than flying taxa in a bivariate linear model, which does not account for any interactive effects. The finding of lower turnover for passively dispersed taxa in a multivariate model could be explained by the fact that passively dispersed taxa are small, and they are thus typically dispersed effectively by wind and animal vectors (Kristiansen, 1996), resulting in low beta diversity. Our analysis likewise suggested that plants that disperse with seeds in the air or with animals (zoochory) have a very low turnover component. These findings are in line with those of Gianuca et al. (2017), who showed that the species replacement (turnover) component may increase with increasing dispersal in heterogeneous environments. The second finding, specifically found for passively dispersed taxa, disagrees with De Bie et al. (2012), who documented that in passively dispersed taxa, the spatial imprint in community compositional variation increased with body size in pond communities. In sum, these findings show that body size–beta-diversity patterns may often be context dependent, and across-taxa generalizations are thus challenging. Therefore, our analysis could not confirm the view that body size per se would have an overwhelming effect on beta-diversity patterns, but rather suggested that body size interacts with dispersal type and

trophic position to affect turnover and nestedness in concert with other ecosystem, geographical and scale-related factors.

Interestingly, we found that trophic position was related to beta-diversity components. For instance, producers had high turnover and total beta diversity, whereas decomposers had low nestedness. One possible explanation for high turnover for producers (except that higher plants had generally low beta diversity) is that they rely on the local environment (e.g., nutrient supply), whereas herbivores and carnivores tend to be controlled by food availability. If the local nutrient supply shows high spatial heterogeneity in the field, for example, this would also be likely to lead to high patchiness in community composition. The beta-diversity patterns for taxa occupying high trophic positions (herbivores and carnivores) are also highly affected by whether they are trophic generalists or specialists (Holt & Hoopes, 2005), with the latter possibly having higher beta diversity because of the spatial distribution of their food availability. Microbial decomposers, such as bacteria and unicellular fungi in our data, are shown to be controlled by the local environment (Davison et al., 2015; Wang et al., 2013). In environmentally heterogeneous ecosystems, it would result in relatively high turnover even if they could be efficiently dispersed among sites.

## 5 | CONCLUSIONS

In conclusion, the present results provide evidence that the degree of species turnover, being consistently the larger component of total beta diversity, and nestedness are related to (a) environmental characteristics, geographical factors and the spatial scale of the study, and that (b) biological features of the focal taxa, such as trophic position, dispersal type and body size, also seem to affect beta-diversity patterns. Even though the collected data originated from highly heterogeneous sources covering a wide range of taxa and ecosystems, we were still able to draw some new general conclusions from these data. We admit, however, that the explanatory power of linear models was fairly low, which might reflect the fact that there is much context dependency across studies. Such context dependency might be related to study design and possibly also to the relative influence of different underlying processes governing beta diversity (i.e., stochastic versus deterministic processes). We emphasize that there is a potential trade-off between the generality of the findings and heterogeneity in the data included in a meta-analysis. Restricting the present analysis to only one realm, for example, would have possibly improved the model fits. However, this would also have resulted in a substantial decrease of the generality of the findings across different realms. In order to reveal the patterns across ecosystems, we tried to be as comprehensive as possible, while at the same time, knowing that models may have relatively low fits. A possible caveat for our analysis is the lack of detailed information about environmental heterogeneity in the study areas (Heino, Melo, & Bini, 2015). Moreover, we had to rely on static snapshots of community data, which are known to exhibit high temporal variability in nature (Fernandes, Henriques-Silva, Penha, Zuanon, & Peres-Neto, 2014). Finally, it is possible that phylogenetic autocorrelation might slightly affect the results, as some data points were perhaps non-independent owing to the shared common ancestry of the organisms. Ants, for example, were well represented in our

data set compared with some other biotic groups. However, we note that within some of the organismal groups, such as in bacteria and algae, beta diversity varied broadly, suggesting that phylogenetic autocorrelation might not be disturbing the major patterns here. As we covered data from various systems within a meta-analysis, we believe that these caveats would not distort our main findings that could only be drawn statistically from large data sets collected from previous published literature. We would urge future studies to test our findings with more specific data sets to gain deeper insights into the variability in the degree of beta diversity that is inherent in nature.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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## APPENDIX : DATA SOURCES

Study	Organism
Aguirre et al. <i>PLoS ONE</i> (2016)	Bats
Aho <i>Ann Zool Fenn</i> (1968)	Macroinvertebrates

(Continues)

## Appendix. (Continued)

Study	Organism
Andersen et al. <i>Insectes Sociaux</i> (2012)	Ants
Arnan et al. <i>J Biogeogr</i> (2006)	Ants
Astorga et al. <i>Global Ecol Biogeogr</i> (2012)	Diatoms
Baselga <i>Global Ecol Biogeogr</i> (2010)	Beetles
Bianchelli et al. <i>Sci Rep</i> (2016)	Meiofauna
Bishop (2012)	Ants
Bishop et al. <i>J Biogeogr</i> (2014)	Ants
Buhk et al. <i>Sci Total Env</i> (2017)	Plants
Burbrink et al. <i>Proc Roy Soc B</i> (2015)	Snakes
Burns et al. <i>AOB Plants</i> (2015)	Bacteria, fungi
Butakka et al. <i>Braz J Biol</i> (2014)	Chironomids
Calatayud et al. <i>J Biogeogr</i> (2016)	Beetles
Calderon-Patron et al. <i>PLoS ONE</i> (2016)	Amphibians
Chazot et al. <i>Am Nat</i> (2014)	Butterflies
Cisneros et al. <i>J Anim Ecol</i> (2015)	Bats
Corti and Datry <i>Freshwater Biol</i> (2015)	Macroinvertebrates
Decaëns et al. <i>Soil Biol Biochem</i> (2016)	Earthworms
Durak et al. <i>Forests</i> (2015)	Trees
Gibb & Cunningham, unpublished	Ants
Gibb & Hochuli <i>Biol Conserv</i> (2002)	Ants
Gibb & Hochuli <i>Oikos</i> (2003)	Ants
Gibb <i>Ecology</i> (2011)	Ants
Gibb et al. <i>Ecology</i> (2017)	Ants
Grossman and Gibb, unpublished	Ants
Gunawardene et al. <i>Forest Ecol Management</i> (2010)	Ants
Hansen et al. <i>Polar Biol</i> (2016)	Plants
Heino & Alahuhta <i>J Anim Ecol</i> (2015)	Beetles
Heino <i>Freshwater Biol</i> (2005)	Macroinvertebrates
Heino <i>Limnol Oceanogr</i> (2008)	Macroinvertebrates
Heino et al. <i>Landscape Ecol</i> (2008)	Macroinvertebrates
Heino et al. <i>Freshw Biol</i> (2015)	Diatoms
Heino et al., unpublished	Macroinvertebrates
Hoffmann & James <i>Austral Ecol</i> (2011)	Ants
Huwer & Wittig <i>Tuexenia</i> (2013)	Plants
Jankowski et al. <i>J Biogeogr</i> (2013)	Birds
Jyrkänkallio-Mikkola et al. <i>J Biogeogr</i> (2017)	Diatoms
Jyrkänkallio-Mikkola et al., unpublished	Diatoms
Keck et al. <i>PLoS ONE</i> (2014)	Fish

(Continues)

## Appendix. (Continued)

Study	Organism
Kokocinski et al., unpublished	Phytoplankton
Lafage et al. <i>Ecol Res</i> (2015)	Spiders
Lappalainen & Soininen <i>Naturwissenschaften</i> (2006)	Fish
Leal et al. <i>J Insect Conserv</i> (2016)	Insects
Longino et al., unpublished	Ants
Lorenzón et al. <i>Comm Ecol</i> (2016)	Birds
Macedo-Reis et al. <i>J Insect Sci</i> (2016)	Beetles
Maloufi et al. <i>Freshwater Biol</i> (2016)	Phytoplankton
McGlynn et al., unpublished	Ants
Menke and Whitcraft, unpublished	Ants
Menke et al. <i>Urban Ecosystems</i> (2010)	Ants
Menke et al. <i>Env Entomol</i> (2015)	Ants
Menke et al., unpublished	Ants
Miranda et al. <i>Checklist</i> (2012)	Ants
Morante-Filho et al. <i>J Anim Ecol</i> (2017)	Birds
Mousing et al. <i>J Ecol</i> (2016)	Phytoplankton
Munyai & Foord <i>J Insect Conserv</i> (2012)	Ants
Mykrä et al. <i>Oikos</i> (2017)	Bacteria, fungi
Olivier & var Aarde <i>J Biogeogr</i> (2014)	Birds, trees
Osunkoya et al. <i>Biol Inv</i> (2011)	Ants
Paknia & Pfeiffer, unpublished	Ants
Parr et al. <i>J Appl Ecol</i> (2004)	Ants
Perez et al. <i>Pedobiologia</i> (2013)	Collembola, plants
Powell et al. <i>Nat Commun</i> (2015)	Bacteria
Pusceddu et al. <i>Mar Environ Res</i> (2016)	Nematodes
Radford et al. <i>Biotropica</i> (2013)	Ants
Ratchford et al. <i>Divers Distr</i> (2005)	Ants
Schiaffiano et al. <i>Env Microbiol</i> (2016)	Microeukaryotes
Si et al. <i>J Anim Ecol</i> (2016)	Birds
Si et al. <i>PLoS ONE</i> (2015)	Birds
Siqueira-Souza et al. <i>Hydrobiologia</i> (2016)	Fish
Soininen & Kõngäs <i>Freshwater Sci</i> (2012)	Bacteria
Soininen et al. <i>Écoscience</i> (2007)	Phytoplankton, zooplankton
Soininen et al. <i>Global Ecol Biogeogr</i> (2016)	Diatoms
Surendran & Vasudevan <i>BMC Ecol</i> (2015)	Amphibians, lizards
Talbot et al. <i>Proc Natl Acad Sci USA</i> (2014)	Fungi
Tedersoo et al. <i>Science</i> (2014)	Fungi

(Continues)

## Appendix. (Continued)

Study	Organism
Teittinen & Soininen <i>Aquat Microbial Ecol</i> (2015)	Diatoms
Teittinen et al. <i>Freshwater Biol</i> (2016)	Diatoms
Teittinen et al. <i>Sci Total Environ</i> (2015)	Diatoms
Teittinen et al., unpublished	Diatoms
Tolonen et al. <i>Freshwater Sci</i> (2016)	Macroinvertebrates
Tolonen et al. <i>Oikos</i> (2016)	Macroinvertebrates
Tonial et al. <i>Br J Biol</i> (2012)	Mammals, birds, reptiles, amphibians
Tonkin et al. <i>Biodiv Conserv</i> (2016)	Macroinvertebrates
Tonkin et al. <i>Oikos</i> (2016)	Invertebrates, spiders, beetles
USA Lake and Stream Ecoregion data	Diatoms, phytoplankton, zooplankton, macroalgae
Walseng et al. <i>Freshwater Biol</i> (2008)	Microcrustaceans
Wang & Soininen, unpublished	Diatoms
Wang et al., unpublished	Bacteria
Wang et al. <i>Nat Comm</i> (2016)	Bacteria
Vasconcelos et al. <i>J Biogeogr</i> (2010)	Ants
Weiss et al. <i>PLoS ONE</i> (2016)	Beetles
Wetzel et al. <i>PLoS ONE</i> (2012)	Phytoplankton
Viana et al. <i>Ecography</i> (2016)	Plants, cladocerans
Vilmi et al. <i>Ecol Ind</i> (2016)	Macrophytes, diatoms, bacteria
Vitorino Junior et al. <i>Freshwater Biol</i> (2016)	Fish
Voutilainen et al., unpublished	Diatoms
Yates et al. <i>PeerJ</i> (2014)	Ants
Zhou et al. <i>Nat Commun</i> (2016)	Bacteria

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