β-diversity scaling patterns are consistent across metrics and taxa

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Abstract

β-diversity (variation in community composition) is a fundamental component of biodiversity, with implications for macroecology, community ecology and conservation. However, its scaling properties are poorly understood. Here, we systematically assessed the spatial scaling of β-diversity using 12 empirical large-scale datasets including different taxonomic groups, by examining two conceptual types of β-diversity and explicitly considering the turnover and nestedness components. We found highly consistent patterns across datasets. *Multiple-site* β-diversity (i.e. variation across multiple sites) scaling curves were remarkably consistent, with β-diversity decreasing with sampled area according to a power law. For *pairwise dissimilarities*, the rates of increase of dissimilarity with geographic distance remained largely constant across scales, while grain size (or scale level) had a stronger effect on overall dissimilarity. In both analyses, turnover was the main contributor to β-diversity, following total β-diversity patterns closely, while the nestedness component was largely insensitive to scale changes. Our results highlight the importance of integrating both inter- and intraspecific aggregation patterns across spatial scales, which underpin substantial differences in community structure from local to regional scales.

Keywords: species composition; dissimilarity; diversity partitioning; nestedness component; spatial turnover; scale dependence; intraspecific aggregation; spatial grain

Introduction

Biodiversity patterns and the mechanisms driving them are inherently scale dependent (Wiens 1989, Levin 1992, McGill 2010a, McGill et al. 2015). Multiple processes determine the distribution and abundance of species, acting upon ecological communities differently at different scales, e.g. climate, local environmental conditions, dispersal and species interactions (MacArthur 1972, Ricklefs 1987, McGill 2010a). Beta (β) diversity quantifies the variation of species composition between assemblages or sites (Whittaker 1960). It is a fundamental component of biodiversity, with implications for community ecology, macroecology and conservation (Whittaker 1960, Anderson et al. 2011, Socolar et al. 2016). As additional habitat types and different environmental features are included in larger geographical areas, β-diversity patterns are expected to be scale dependent (Koleff et al. 2003, Tuomisto 2010a, Barton et al. 2013). However, while the scaling properties of species richness have received substantial attention (e.g. Rosenzweig 1995; Harte et al. 2009; Storch et al. 2012), the scaling of β-diversity is less understood, with a lack of theoretical predictions about the form of β-diversity scaling patterns (Koleff et al. 2003, Gaston et al. 2007, Barton et al. 2013).

Analyses of β-diversity can be used to address two sets of questions: variation among sites within a given spatial extent, habitat type or experimental treatment (*multiple-site* β-diversity) *vs* differences between sites along a spatial or environmental gradient (*pairwise* dissimilarities), thus yielding two conceptual types of β-diversity (Anderson et al. 2011). The first approach derives aggregate measures of β-diversity across all sites regardless of their location (i.e. not spatially explicit), while the second approach typically regresses pairwise site comparisons *vs* geographic distance (distance-decay relationship (DDR); Nekola & White 1999; Morlon et al. 2008). DDR are often well fitted by exponential or power law curves, and β-diversity is then summarized as the rate of change from this curve (Nekola and McGill 2014). Additionally, β-diversity may reflect two underlying phenomena – turnover and nestedness. The turnover component represents the replacement of species between sites, whereas the nestedness-resultant component occurs due to changes in species richness – sites with fewer species are strict subsets of richer sites (Harrison et al. 1992, Koleff et al. 2003, Baselga 2010). Nestedness and turnover are generated by different processes – species loss and species replacement respectively – therefore quantifying their relative contribution can provide insights into the mechanisms underlying β-diversity across spatial scales

(Baselga 2010, Svenning et al. 2011). However, little is known about how the two components change across different scales. Here, we examine both *multiple-site* and pairwise β-diversity, as well as their components, taking advantage of the framework developed by Baselga for presence-only data (2010), in order to understand the scaling properties of β-diversity.

Expectations for the scaling of β-diversity

The measurement of β-diversity is affected by the spatial scale of observation, both in terms of grain and extent (Preston 1948, Wiens 1989, Nekola and White 1999, Mac Nally et al. 2004, Qian 2009, Keil et al. 2012, Steinbauer et al. 2012, Barton et al. 2013, Nekola and McGill 2014). For small grain sizes compared to the overall study extent, even close sampling units might be very dissimilar in their species composition, due to stochastic sampling effects and high variability in species occupancy patterns. As grain size increases, mean environmental variability decreases as a result of spatial averaging, and the probability of detecting more rare species increases (Wiens 1989, Levin 1992, Gaston et al. 2007, Keil et al. 2012, Barton et al. 2013). Hence, *multiple-site* β-diversity is expected to decrease as grain increases. But what is the functional form of this relationship? And are the patterns system or taxon specific (Barton et al. 2013)? Our analysis provides the first attempt to build empirical β-diversity scaling curves – akin to the triphasic Species-Area Relationship (SAR; Williams 1943; Rosenzweig 1995; Storch et al. 2012), and the first assessment of the generality of these scaling patterns.

Pairwise dissimilarities are also expected to decrease as grain size increases, but previous studies have reported conflicting results. For instance, lower DDR rates (Nekola and White 1999) and lower β-diversity (Keil et al. 2012) were reported for larger grains. In contrast, Morlon et al. (2008) found that grain size only affected rates of decay at the smallest grain analysed, while no consistent trend was found by both Steinbauer et al. (2012) and Zacaï et al. (2016). This suggests that the influence of grain size on DDR cannot be easily predicted, and might be context and/or taxa dependent. However, these studies have all employed different approaches, varying total extent and/or grain, and analysing the patterns at different spatial scales (continents to plots). Hence, employing a systematic multiscale approach across multiple taxa can help disentangle scale effects and ecological patterns.

A few studies have analysed turnover and nestedness components' patterns at large spatial extents for specific taxa, with their relative contributions being apparently contingent on the context and scale investigated (Baselga 2010, Svenning et al. 2011, Wen et al. 2016), but a general investigation of turnover and nestedness relative contributions independent of latitudinal, longitudinal or environmental gradients is still lacking. Turnover can be expected to be lower between larger sampled areas and for more vagile organisms. It may be that the nestedness component is less relevant between smaller sampled areas, where turnover may be the dominant driver of β-diversity. On the other hand, nestedness could also represent a smaller portion of β-diversity in scenarios with high dispersal rates. Thus, it is not clear how grain could affect the relative importance of the two components, with possible interactions resulting from other mechanisms, such as metacommunity dynamics (Leibold et al. 2004, Si et al. 2015, Tonkin et al. 2016, Schuler et al. 2017, Gianuca et al. 2017).

Here, we establish a scale gradient within 12 communities encompassing different taxa to systematically assess β-diversity scaling patterns. We undertake the first empirical assessment of *multiple-site* β-diversity scaling with sampled area. Additionally, we consistently investigate the behaviour of pairwise dissimilarities across the scale gradient, by testing the hypothesis that DDR rates become steeper (more pronounced) as grain size decreases. Finally, we test whether turnover decreases with area sampled, while exploring the behaviour of the nestedness component.

Material and Methods

To quantify community dissimilarity, we used the additive partition framework proposed by Baselga (2010), where the Sørensen index represents total β-diversity accounting for all aspects of compositional variation, the Simpson index represents turnover, i.e. species replacement independent of species richness gradients, and their difference represents a measurement of dissimilarity due solely to species richness differences, i.e. the nestedness-resultant component:

$$\beta_{Sørensen} = \beta_{Simpson} + \beta_{Nestedness-resultant}.$$

We follow the same notation as Baselga (2010), using upper-case letters for the *multiple-site* metrics (β_{SOR}, β_{SIM}, β_{NES}), and lower-case letters for pairwise dissimilarities (β_{sor}, β_{sim}, β_{nes}). We emphasize that we examine the component of β-diversity due to differences in species richness, not nestedness itself (Baselga 2010, 2012). Gamma diversity (i.e. the total number of species sampled in the overall extent) was assumed constant for each dataset, and because our goal was not to estimate latitudinal gradients of β-diversity, we did not employ a null model approach (Tuomisto 2010b, Ulrich et al. 2016, Socolar et al. 2016). All analyses used presence-only data and were performed using the statistical software R (R Core Team 2017).

Empirical Data

We analysed 12 datasets comprising different taxa, namely birds, fish, benthos and trees. We selected 11 datasets from the BioTIME database (Dornelas et al. 2018) with spatial extent larger than 150 000 km^2 and for which the unique sampling locations were distributed across the study area so that the random splitting of the total extent would not result in portions without sampling locations (see next section). We used data from a single year for each dataset (the year with the most and more evenly distributed sampling locations). We also analysed the Forest Inventory and Analysis Database (FIA; http://fia.fs.fed.us/; USDA Forest Service 2010; Woudenberg et al. 2010), as we wanted to include tree community data in our analysis; we obtained these data using the EcoData Retriever (http://data-retriever.org; Morris and White 2013, McGlinn and White 2015). These empirical datasets cover a wide

range of sampling grains (0.0001 to 400 km^2) and total spatial extents (167 455 to 16 663 141 km^2). The full list of datasets and sources can be found in Table 1.

Implementing the scale gradient

We established a scale gradient by using the fixed extent of the study area and systematically partitioning this area into smaller portions, thus varying "grain" size as follows. We drew a circle encompassing all the sampling locations from the community data and centred on the centroid of the sampling locations. A random point from the circle was selected to split the circle into halves, thirds, quarters, eights and sixteenths, using the initial random point from the bisection as reference (Fig. 1). We subsampled to obtain an equal number of samples in each subsection and pooled species abundances across the retained samples within each section. We then calculated β-diversity metrics at each level. Each study was randomly split ten times, to assess the generality of our results focusing on effects of scale independently of latitudinal or longitudinal effects. Finally, we calculated β-diversity between all the individual samples, representing the lowest level of the scale gradient. This procedure thus yielded six scaling levels covering several orders of magnitude (we were not able to establish more levels after splitting the extent into 16 sections since the sampling locations were not evenly distributed across the extents, which would lead to having empty sections or sections containing only one or two samples).

The sample areas created as described above were not exhaustively sampled (which would be a logistical impossibility). Thus, we calculated the area of the sample in two ways, bracketing the upper and lower bounds of what could reasonably be called the sampled area. First, the areas sampled were calculated using convex hull polygons encompassing the sampling locations within each section, using package rgeos (Bivand and Rundel 2016) (Fig. 1). At each level, sampled area was estimated as the minimum of the convex hull areas – the estimated metrics are representative of the smallest area. Additionally, we calculated area sampled as grain size * number of samples, representing the actual area sampled. For the lowest level of the scale gradient, we considered the grain size of individual samples, assuming a value from a similar study if the exact information was not available (Table 1). Since the range of grains analysed covers several orders of magnitude, our results are not contingent on the exact grain size at the smallest scale. Geographic distances were calculated in km as the distance between the centroids of each

section, and between all the sampling locations for the grain level, using package sp (Pebesma and Bivand 2005) (Fig. 1).

Multiple-site β-diversity

To assess how *multiple-site* dissimilarity varied with grain, we used function beta.sample() in betapart package (Baselga and Orme 2012, Baselga et al. 2017) to calculate total β-diversity, turnover and nestedness components. beta.sample() randomly selects a specified number of sites to generate distributions of the *multiple-site* dissimilarity measures, thus allowing to compare the different scaling levels using an equal number of sites. To fully explore scaling, we sampled two sites at each level, drawing 1000 random samples. We fitted two models to the *multiple-site* β-diversity scaling curves. First, we used generalized nonlinear least squares to fit a power law to each metric as a function of area (i.e. Dissimilarity ~ 1-(a*Area$^{\wedge b}$)), using function gnls() from the nlme package (Pinheiro et al. 2016). Second, we fitted a linear model to the logit transformation of dissimilarity values as a function of log10(Area). To illustrate that the patterns are not contingent on using estimates from a single trial, we compared the median β_{SOR} values across all the trials (excluding the last one) with the values used in the analysis.

Pairwise β-diversity

We used function beta.pair() in betapart (Baselga and Orme 2012, Baselga et al. 2017) to obtain pairwise dissimilarities between the sections at each scaling level and between all the sampling locations for the grain level (pairwise dissimilarities represent the opposite of distance-decay of similarity). For the datasets with over 5000 individual samples, we randomly sampled 2000 samples for the grain level models, due to the very high number of pairwise comparisons (Table 1). We fitted negative exponential models to each dissimilarity metric *vs* geographic distance (Nekola and McGill 2014) via GLM using the decay.model() function from betapart, which also implements a permutation test to assess significance (n=100) (Baselga et al. 2017, Gómez-Rodríguez and Baselga 2018). We tested if the slopes and intercepts increased as grain decreased by bootstrapping the parameters using the function boot.coefs.decay() in betapart (1000 bootstraps; for the grain level only 100 bootstraps were used due to the very high number of calculations to perform). Finally, we assessed if coefficients for turnover (β_{sim}) were higher than for

nestedness (β_{nes}) within each scaling level by calculating the probability of obtaining the opposite result by chance, by comparing the bootstrap parameter distributions. These procedures were not performed for the bisection, 1/3 and 1/4 levels due to the small number of pairwise comparisons available to accurately assess DDR.

Results

Multiple-site β-diversity

Multiple-site β-diversity scaling curves were very similar across the communities analysed, with β_{SOR} decreasing with sampled area according to a power law (Fig. 2; Table S1). As these patterns were consistent across the ten random splitting trials (Supplementary Figs. S1 and S2), we report the results for a single split. Some communities exhibited more contracted curves along the y-axis, i.e. for the larger areas sampled β_{SOR} was <0.2 (e.g. SCRT, MBBA, and NPGO), whereas for others it was ~0.4-0.8 (e.g. RLS_F, RLS_I, and FIA). β_{SIM} exhibited a similar pattern, representing the largest portion of β-diversity across the scale gradient and for all the communities. β_{NES} seemed to be relatively insensitive to changes in area sampled, and always had a smaller contribution to β-diversity, although it increased slightly for some communities as area increased (Fig. 2). The results were qualitatively very similar when using area sampled as grain * number of samples (Fig. S3). Model fitting indicated that a power law always provided the best fit according to AIC (Fig. S4). Moreover, the estimated power law coefficients fell in a relatively narrow parameter space (Fig. S5), and in many situations were not statistically different between datasets.

Pairwise β-diversity

We used a single random trial since there was relatively small variability in the estimated coefficients among trials, and restricted our comparisons to the lowest levels of the scale gradient. At a given level, β_{sor} increased with geographic distance, and as the scale level increased overall dissimilarity decreased (Figs. 3 and S6). While β_{sim} followed β_{sor} patterns closely, β_{nes} exhibited significant negative slopes at the grain level, and did not show a consistent trend across the other levels, but always exhibited shallower

slopes (Figs. 3 and S6). In general, pairwise-vs-distance slopes remained relatively unchanged as grain decreased, and for several datasets were not different between scaling levels, while intercepts were consistently higher comparing grain *vs* 1/16 and *vs* 1/8 for β_{sor} and for β_{sim} (Figs. 3 and 4; note the different scales for slopes and intercepts and across the metrics). For β_{nes}, grain had no effect for both parameters (Fig. 3). Turnover accounted for the largest portion of β-diversity across all the communities and the scale gradient (Fig. S6). Pairwise comparisons between the bootstrapped coefficients for β_{sim} and β_{nes} showed that both slopes and intercepts were consistently higher for turnover (Fig. 4).

Discussion

Our study - the first comprehensive empirical analysis of β-diversity scaling patterns - reveals a remarkable consistency across taxa, with *multiple-site* β-diversity decreasing with area sampled according to a power law. Furthermore, for pairwise comparisons, the rates of increase of dissimilarity with distance remained largely unchanged across scales spanning several orders of magnitude, while grain affects overall dissimilarity values. In both analyses, turnover accounted for most of β-diversity across all the communities, showing similar scaling properties to total dissimilarity, with the nestedness component being lower and relatively insensitive to large changes in grain. In general, the smaller the area sampled (and for more dispersal limited organisms), the more dissimilar the sites being compared will be (Nekola and White 1999, Mac Nally et al. 2004, Barton et al. 2013). This is consistent with what we found in both our analyses: a decrease in *multiple-site* dissimilarity as grain increased, and higher overall pairwise dissimilarity for smaller grains (consistently higher intercepts for lower levels of the scale gradient). As grain size increases, more species are shared between the sampled areas, and micro-environmental differences are attenuated. Moreover, larger areas will harbour more species and pooling samples to obtain coarser grains results in larger samples and consequently increased probability of sampling more rare species.

Multiple-site β-diversity decreases as a power law of sampled area for all the communities analysed, when some variability could be expected due to specific ecological and/or environmental underlying factors (Barton et al. 2013). In addition, both types of β-diversity exhibited regular patterns, revealing a

remarkable consistency in β-diversity scaling properties across taxa. The datasets analysed comprise very different taxa, with different ecological and dispersal characteristics. Moreover, the datasets analysed cover a wide range of spatial extents, grain sizes and species richness, suggesting that our results are robust to large variation in these fundamental aspects of ecological studies. Our findings can be related to two fundamental patterns of ecology: species spatial aggregation patterns and the triphasic SAR, which we discuss in turn.

One of the three assumptions common across unified biodiversity theories is that conspecific individuals are spatially aggregated (McGill 2010b). Spatial aggregation has been particularly studied for terrestrial plants and at smaller spatial scales (Condit et al. 2000, 2002, Plotkin and Muller-Landau 2002, Plotkin et al. 2002, Morlon et al. 2008). Conspecific aggregation affects the expected similarity between samples within a regional landscape (Plotkin and Muller-Landau 2002) and DDR rates (Morlon et al. 2008). Our results suggest that conspecific aggregation is a plausible mechanism across spatial scales spanning several orders of magnitude, from very small local samples to very large regional areas, and across taxonomic groups. However, two further aspects could be relevant in framing our results and the effects of species spatial aggregation. First, Morlon et al. (2008) noted that the homogeneous Poisson-cluster Process was unable to completely reproduce distance-decay relationships in empirical forest plots, particularly for more heterogeneous landscapes. This process assumes a single scale of aggregation, a constant density of conspecifics across the landscape, and ignores interspecific spatial correlations; these assumptions are likely violated in natural systems. Second, we found a different functional form of the expected similarity with increasing area to that derived by Plotkin & Muller-Landau (2002). Given the consistency of the β-diversity scaling patterns we found and the range of scales analysed (and presumably the high habitat heterogeneity underlying the scale gradient), together with the two above inconsistencies, our results suggest that neither the negative binomial nor a Poisson-cluster Process will be able to adequately describe (dis)similarity patterns across scales (from local to regional scales). We suggest that such inability may be attributable to the underlying assumption of independent species placement (i.e. species randomly distributed regardless of other species), which is unlikely to hold across scales. Morlon et al. (2008) also suggested that interspecific spatial aggregation could potentially affect distance-decay relationships by indirectly influencing species abundances and intraspecific aggregation, while noting that the inability of the Poisson Cluster model in reproducing empirical patterns would reveal the need of

incorporating more heterogeneity into the models. We suggest that inter-species aggregation is also a relevant driver of the patterns we found, particularly at larger spatial scales.

SARs describe the increase in species richness as area sampled increases. In logarithmic space, SARs are concave for small scales (downward accelerating), become linear for intermediate scales, and then convex for larger scales (upward accelerating), indicating that distinct regions are then being sampled (Rosenzweig 1995). Intuitively, the transition between these distinct phases (i.e. inflection points) can be related to the dispersal ability of the taxa studied. Since in all our datasets the total extent sampled was much larger than the areas at which the inflection point indicates progressively increasing slopes (Fig. S7), one can expect relatively high β-diversity (mainly due to turnover) even for very large samples (e.g. the bisection level), since each section is likely to contain some species not present in the other section. In other words, if the total spatial extent roughly coincided with the inflection point, the two random bisections would more likely contain the entire set of species present in the region, and β-diversity would be ~0. Our results are consistent with this expectation. Furthermore, the dataset with the largest difference between the inflection point and the overall extent is RLS Invertebrates (RLS_I), which exhibited the overall highest β-diversity values across the scale gradient. Moreover, of the datasets analysed, RLS Invertebrates is arguably the most dispersal-constrained community, further suggesting that both dispersal ability and spatial extent underlie the patterns found. Nonetheless, we have not explicitly explored how dispersal ability could be linked to our results, thus further research is still necessary to evaluate which species traits underlie the patterns found, and furthermore if such patterns would be consistent for other taxa and ecosystems. Overall, our results suggest the spatial extent (and potentially the underlying habitat heterogeneity), dispersal abilities, and both intra- and inter-species aggregation patterns as important drivers of β-diversity scaling patterns.

Multiple-site β-diversity

There were some differences among the scaling curves, namely a contraction along the y-axis for some communities. In other words, some communities still showed very high *multiple-site* β-diversity even for very large sampled areas. β_{SOR} at the bisection level was particularly high for the RLS Fish and Invertebrates (RLS_F; RLS_I), and FIA datasets (Fig. 2). For more heterogeneous landscapes and for

organisms with lower dispersal ability, sampled areas are expected to be more dissimilar (Qian 2009, Si et al. 2015). While the spatial configuration of the RLS data could also potentially affect *multiple-site* β-diversity patterns, and we have not tested for this effect (sampling sites distributed around Australia *vs* contiguous cloud of more or less dispersed sampling locations across the spatial extent), the FIA dataset exhibited similar patterns, which lends support to the argument that ecological properties of the different taxa, rather than the spatial distribution of the individual sampling locations, more strongly affected *multiple-site* β-diversity patterns in our analysis, along with the influence of the overall extent sampled, as discussed above.

Pairwise β-diversity

The rates of pairwise-vs-distance relationships remained relatively unchanged as grain decreased, across very large ranges of area sampled, while intercepts increased with decreasing grain size. These results contrast with previous reports (Keil et al. 2012, Steinbauer et al. 2012), but are in accordance with Morlon et al.'s (2008) results showing that grain affected overall similarity values, rather than DDR rates, except at the smallest sampled area. Our results are consistent with Morlon et al.'s, although we found no significant differences among the scaling levels for some of the datasets (Fig. 4). However, the range of areas investigated differs greatly between our studies: grain values ranged between 0.0004 - 6.25 ha in Morlon et al., while our scale gradient spanned much larger areas, with a very sharp increase from the smallest to the subsequent levels. Since Morlon et al.'s range is much narrower, we can reconcile both studies in that DDR rates seem to be overall robust to large variations in area sampled, while those variations more strongly affect overall dissimilarity (which is also aligned with Keil et al.'s results). This suggests that DDR rates alone are not a good indicator of compositional patterns across scales, while intercepts provide a better assessment of dissimilarity across spatial scales (Morlon et al. 2008, Gómez-Rodríguez and Baselga 2018), as do *multiple-site* dissimilarity metrics.

Our results differ from those of Keil et al. (2012) and Steinbauer et al. (2012), but we attribute this to the very different spatial frameworks between our studies. Firstly, both grain and extent were allowed to vary in those studies. Moreover, in Steinbauer et al.'s analysis, the distance between plots was kept constant while increasing plot size, and slopes were more strongly affected by varying extent than grain size. In

our analysis, we used a fixed extent, so that community data was sampled from a fixed species pool, while the areas sampled and the distance between them were unconstrained. This isolates variation in β-diversity from variation in gamma diversity. Secondly, we did not impose static grids over regional or continental extents, but analysed dissimilarity patterns across a scale gradient spanning several orders of magnitude. Finally, we used data collected with a high degree of spatial resolution, from many small representative samples, rather than incidence data across large grid sizes, atlases or simulated data. However, one caveat of our study was that we were unable to fully explore the scale gradient for the pairwise-vs-distance analysis, as we could not include the higher levels of the scale gradient. Nonetheless, our results showed that large increases in grain had no or little effect on DDR rates, but did affect overall dissimilarity; i.e. grain size, rather than the distance between sites, more strongly affected dissimilarity patterns across the scale gradient.

Higher intercepts indicate higher β-diversity, since even closer locations exhibit low similarity; this can be related to higher habitat heterogeneity in those communities, and/or linked to low dispersal abilities of the organisms (Nekola and White 1999, Morlon et al. 2008). Both *multiple-site* and DDR intercepts are good indicators of how dissimilarity is affected by sampling grain. For some datasets, DDR slopes differed more between scaling levels, namely for the RLS datasets and SCRT. The RLS survey datasets are the two most diverse in our analysis in terms of species richness; moreover, the sampling locations are distributed around Australia, which encompasses distinct ecoregions. Thus, one could expect the rates of dissimilarity between very small sample sizes at the grain level to differ to grain sizes orders of magnitude larger. On the other extreme, SCRT is the dataset with fewer species, so sampling effects (e.g. not sampling the rarest species) could explain the differences in DDR rates. Nonetheless, the overall pattern across all the datasets is that grain affected intercepts more strongly than slopes, suggesting that including information about variation in intercepts (i.e. dissimilarity at the smallest scale) is fundamental to understanding dissimilarity patterns (Morlon et al. 2008, Gómez-Rodríguez and Baselga 2018).

β-diversity components

Partitioning β-diversity into turnover and nestedness revealed that the two components exhibit divergent spatial patterns, with turnover strongly driving total β-diversity patterns, for all the communities and across the scale gradient (see also Soininen et al. 2017). In contrast, the nestedness component

contribution was systematically low and generally scale insensitive. Since turnover followed the total

dissimilarity pattern very closely, the nestedness component had to exhibit a contrasting pattern, due to

the additive nature of the partitioning framework (Baselga 2010). Interestingly, nestedness decreased with

geographic distance only at the lowest level of the scale gradient (and occasionally also at the next level),

being seemingly unaffected when calculating dissimilarity between sections at higher levels. It is not

straightforward to establish expectations for how the nestedness component should behave across scales,

since several interacting factors must be considered. For instance, the relative balance between turnover

and nestedness depends both on dispersal rates and on environmental heterogeneity (Gianuca et al. 2017).

Complementary analyses including dispersal ability and habitat heterogeneity might provide further

insights to help discern how the two components are expected to behave (Soininen et al. 2017). We note

here that although β-diversity partitioning has sparked some debate (Almeida-Neto et al. 2012, Carvalho

et al. 2012), the framework used here was shown to adequately measure the portions of dissimilarity

derived exclusively from species replacement and nested patterns (Baselga 2012, Baselga and Leprieur

2015).

The fact that species replacement, rather than change in species richness, was the main driver of

compositional change across the scale gradient offers important insights for the underlying processes

driving β-diversity at different spatial scales. It also has implications for both our understanding of

spatiotemporal dynamics of biodiversity change and conservation (Baselga 2010, Dornelas et al. 2014,

McGill et al. 2015, Magurran et al. 2015, Socolar et al. 2016), highlighting that substantial changes in

community composition might be occurring, despite species richness remaining seemingly stable. A

recent meta-analysis by Soininen et al. (2017) also found turnover to be the dominant component of β-

diversity across different latitudes, spatial extents and taxa. A general understanding of the relative

contribution of each component to β-diversity patterns across spatial scales has relevant implications for

conservation strategies, specifically concerning the number and size of areas to be protected depending on

whether species turnover or species richness differences are dominant (Baselga 2010, Socolar et al. 2016).

Our study represents the first investigation of turnover and nestedness components contributions

independent of latitudinal, longitudinal or environmental gradients, revealing consistent patterns for the

communities analysed.

Conclusions

We found highly regular β-diversity scaling patterns across the communities analysed, with *multiple-site* dissimilarity decreasing with grain according to a power law, and with turnover being the main driver of β-diversity across scales spanning several orders of magnitude. We suggest that the scaling patterns found are likely underpinned by the interplay of species dispersal abilities, intra- and inter-specific spatial aggregation patterns, as well as the overall diversity being sampled (as exemplified by the potential link with the SAR). Given the current need to quantify how biodiversity is changing in the Anthropocene, it is of critical importance that we understand how spatial scale can influence changes regarding community structure and composition. Our findings provide valuable insights to understanding and synthetizing β-diversity scaling patterns across taxa and ecosystems.

Author contributions

L.H.A. and M.D. designed the study, L.H.A. assembled the data and performed all the analyses. L.H.A. wrote the first draft of the manuscript; all authors have discussed the results and contributed extensively to the final manuscript.

Data Accessibility statement: All the datasets used in this study can be accessed through either the

BioTIME database or the EcoData Retriever, or alternatively from the original sources cited.

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Figure Legends

Figure 1. Schematic representation of the scale gradient, showing an example of how an encompassing

circle was drawn and a random point was selected to establish bisections (a and b) and thirds (c – e). For

multiple-site β-diversity scaling curves, the smallest section area at each level was used (b and c); for

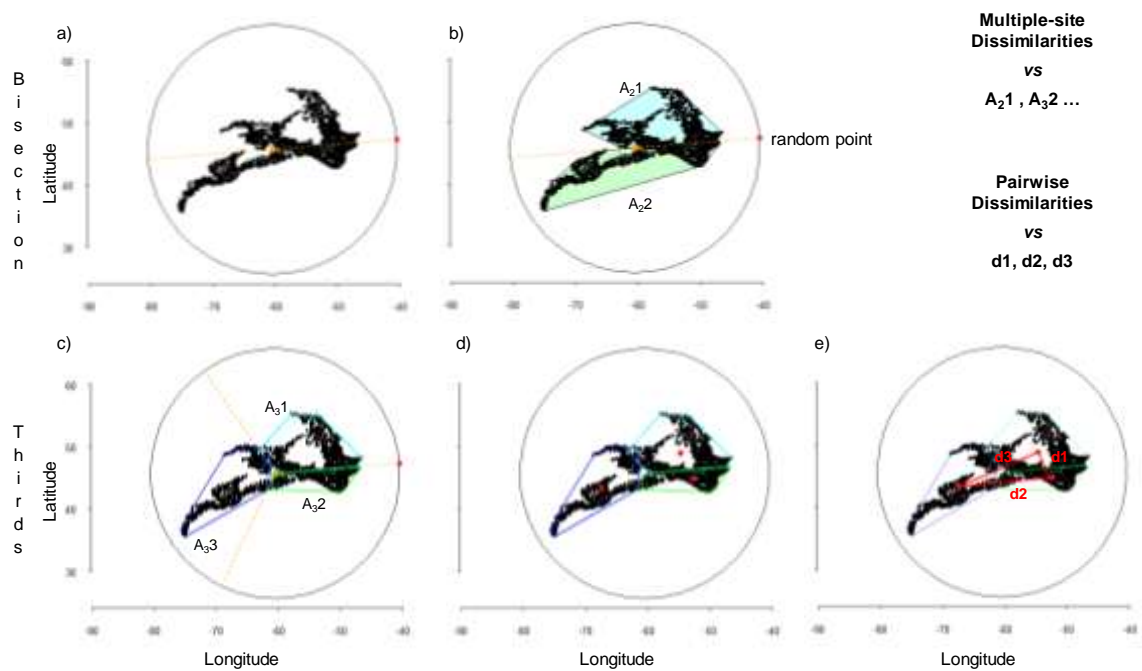pairwise β-diversity, the distances between the centroids of each section were calculated (d and e).

Figure 2. *Multiple-site* β-diversity scaling curves, showing the decrease of β_{SOR} and the turnover component β_{SIM} with increasing grain according to a power law (on a semi-log plot). The points represent the *multiple-site* dissimilarity values for each level of the scaling gradient (1/2, 1/3, 1/4, 1/8, 1/16 of the total extent; and sampling grain), where the bisection level has the largest area, and the grain size represents the smallest area. The lines represent the power law model fitted to each dataset for each dissimilarity metric, which provided a better fit than a linear logit model according to AIC (Fig. S4). The area plotted is the minimum convex hull polygon value at each level; Fig. S3 shows the scaling curves with area calculated as grain * number of samples.
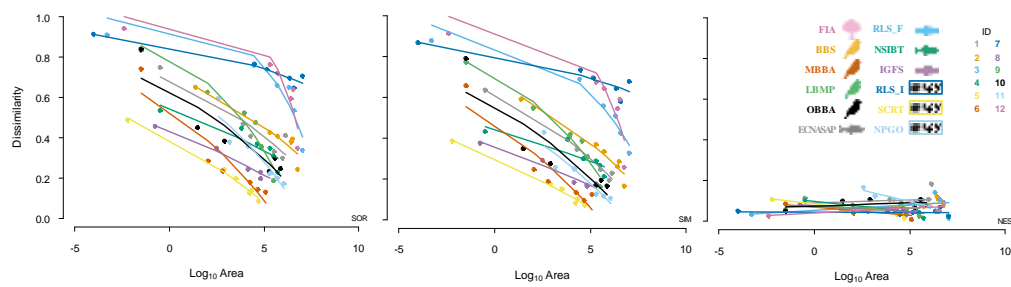
Figure 3. Pairwise dissimilarities *vs* distance negative exponential models parameters ((a) slopes and (b) intercepts) as a function of the scaling level, combining all the random splitting trials and datasets; note the differences in the y-axis scales for the two parameters. For this analysis, we explored only three scaling levels (grain; 1/16; and 1/8) because the higher levels in the scale gradient contain too few pairwise comparisons to confidently estimate DDR.
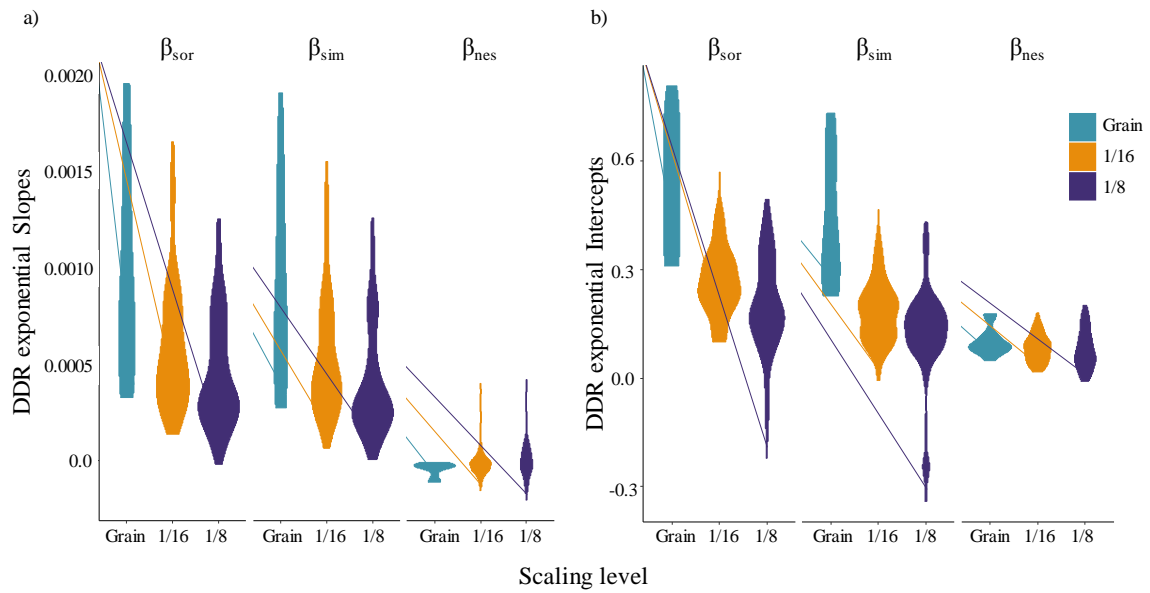
Figure 4. Bootstrapped distributions of the negative exponential models parameters used to describe pairwise dissimilarities as a function of distance for β_{sim} and β_{nes} (note the differences in the x-axis scales between slopes and intercepts and between metrics). Each row is identified by the corresponding dataset abbreviation as in Table 1.
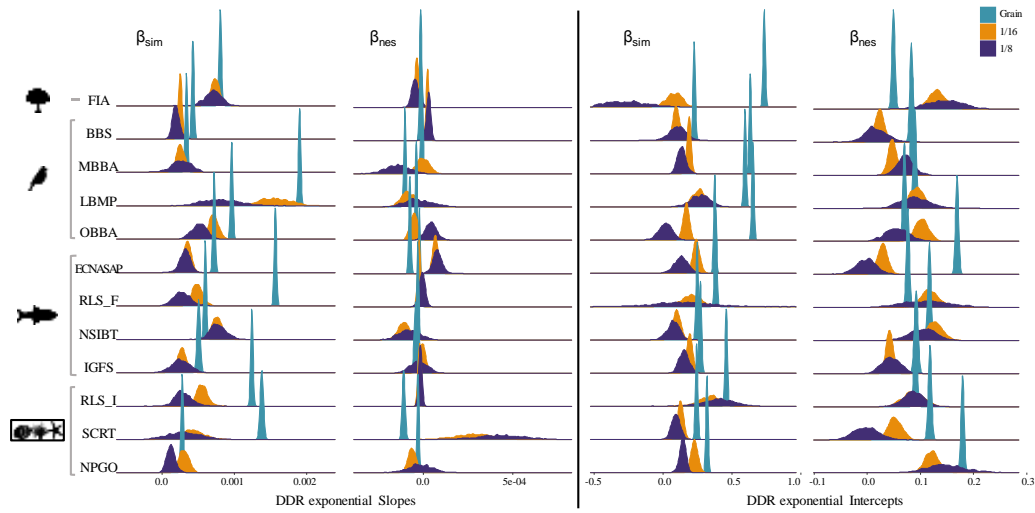
Table Legend

Table 1 – Community data with the corresponding taxon, species richness, spatial extent, grain and data source.

Dataset Title	Abbreviation	Taxon	Usage notes	Spatial extent (km^2)	Grain (km^2)	Number of species	Number of samples	Reference
Forest Inventory Analysis	FIA	Trees	2013; excluded Alaska	16 663 141	0.004047	305	19 427[¥]	(USDA Forest Service 2010, Woudenberg et al. 2010)
North American Breeding Bird Survey	BBS	Birds	2015; USA data only (excluded Alaska)	13 104 786	25.42715	521	2 420	(Pardieck et al. 2016)
Maritimes Breeding Bird Atlas	MBBA	Birds	2009	480 235	0.031416*	163	3 243	(NatureCounts a)
Landbird Monitoring Program	LBMP	Birds	2004	1 057 570	0.031416*	229	5 107[¥]	(USFS)
Ontario Breeding Bird Atlas	OBBA	Birds	2003	3 545 420	0.031416	233	19 611[¥]	(NatureCounts b)
East Coast North America Strategic Assessment	ECNASAP	Fish	1994	7 229 693	0.33336	110	2 101	(Brown et al. 2005)
Reef Life Survey: Global reef fish dataset	RLS_F	Fish	Spatial subset around Australia	572 747	0.0005	1 847	6 666[¥]	(Edgar and Stuart-Smith 2014a, b)
ICES North Sea International Bottom Trawl Survey for commercial fish species	NSIBT	Fish	2011	2 726 171	0.33336*	131	688	(DATRAS 2010a)
Irish Ground Fish Survey for commercial fish species	IGFS	Fish	2004	967 879	0.177792	207	163	(DATRAS 2010b)
Reef Life Survey: Invertebrates	RLS_I	Invertebrates	Spatial subset around Australia	572 747	0.0001	1 013	6 817[¥]	(Edgar and Stuart-Smith 2008, 2014b)
Snow crab research trawl survey database	SCRT	Benthos	2009	167 455	0.00642	32	354	(Wade 2011)
North Pacific Groundfish Observer	NPGO	Benthos	1993	6 794 596	400	220	1 007	(North Pacific Groundfish Observer Program)

*Grain was approximated to similar studies; [¥] indicates 2000 random samples were used for the grain level pairwise dissimilarities analysis.