ECOLOGICAL SOUNDING

The spatial scaling of beta diversity

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ABSTRACT

Beta diversity is an important concept used to describe turnover in species composition across a wide range of spatial and temporal scales, and it underpins much of conservation theory and practice. Although substantial progress has been made in the mathematical and terminological treatment of different measures of beta diversity, there has been little conceptual synthesis of potential scale dependence of beta diversity with increasing spatial grain and geographic extent of sampling. Here, we evaluate different conceptual approaches to the spatial scaling of beta diversity, interpreted from 'fixed' and 'varying' perspectives of spatial grain and extent. We argue that a 'sliding window' perspective, in which spatial grain and extent covary, is an informative way to conceptualize community differentiation across scales. This concept more realistically reflects the varying empirical approaches that researchers adopt in field sampling and the varying scales of landscape perception by different organisms. Scale dependence in beta diversity has broad implications for emerging fields in ecology and biogeography, such as the integration of fine-resolution ecogenomic data with large-scale macroecological studies, as well as for guiding appropriate management responses to threats to biodiversity operating at different spatial scales.

Keywords

Alpha diversity, community, dissimilarity, gamma diversity, spatial extent, spatial grain, Sørensen, species turnover.

INTRODUCTION

Beta diversity is an important concept used in its broadest sense to describe variation in species identities from site to site (Anderson *et al.*, 2011). As a consequence, beta diversity is fundamental to community ecology and underpins conservation theory and practice (Gering *et al.*, 2003; Kraft *et al.*, 2011). The concept itself is often thought of in coarse (but intuitive) terms as 'species turnover'. Yet, a surprisingly wide variety of definitions and approaches to the analysis of beta diversity has emerged since Whittaker (1960) first introduced the concept. Since then, there has been an explosion of reviews and commentaries by diverse authors attempting to clarify important issues of analysis and terminology, with much recent success (e.g. Jost, 2007; Jurasinski *et al.*, 2009; Baselga, 2010b; Tuomisto, 2010a, b; Anderson *et al.*, 2011). Unfortunately, the same level of attention has not yet been given to other, equally fundamental, conceptual issues surrounding scale dependence in the patterns and processes driving variation in beta diversity among sampling units at different spatial scales of observation, or among communities of organisms that perceive their environment at different spatial scales. As a consequence, there is as yet no general framework for describing the spatial scaling of beta diversity.

Ecologists typically measure scale in terms of grain and extent (Nekola & White, 1999; Whittaker *et al.*, 2001). Within biogeography, there is extensive evidence for variation in the spatial patterns and processes driving alpha diversity at different spatial grains and extents (Palmer & White, 1994; Rosenzweig, 1995; Whittaker *et al.*, 2001; Field *et al.*, 2009). For example, at very fine scales, alpha diversity increases quickly with spatial extent due to high variation in stochastic species occupancy patterns among sampling units, and deterministic variation in species responses to habitat heterogeneity. At intermediate scales, diversity increases more slowly with spatial extent as fewer new species are encountered relative to the regional pool. Meanwhile, at very large scales, species diversity increases more quickly again across biogeographic regions with distinct geological barriers and evolutionary histories (Whittaker *et al.*, 2001; Hortal *et al.*, 2010). Although there is recognition that spatial grain and extent also have important influences on the measurement and

interpretation of beta diversity (Nekola & White, 1999; Steinbauer *et al.*, 2012), the patterns and processes shaping the spatial scaling of beta diversity have not yet been thoroughly explored.

There are two main approaches that can be used to conceptualize spatial variation in beta diversity: (i) the distance-decay of community similarity, and (ii) the partitioning of species diversity into alpha and beta components. Distance-decay studies regress pair-wise measures of sample-unit similarity against pair-wise spatial distance, and parameterize a 'slope' that indicates the relative change in compositional similarity through geographic space (Nekola & White, 1999). Diversity partitioning studies, meanwhile, derive aggregate measures of beta diversity (e.g. Whittaker's, 1960, multiplicative beta or Lande's, 1996, additive beta) from the relationship between mean alpha diversity in a sample unit of a given grain versus gamma diversity from all sampling units at their combined extent, and indicates the average diversity not found in any one sampling unit (Veech & Crist, 2010). The effective number of compositionally dissimilar sampling units (the 'true' beta diversity of Tuomisto, 2010a) could be applied in a similar (multiplicative) partitioning approach. When applied across multiple scales of sampling (i.e. sampling units that are progressively aggregated upwards), diversity partitioning can thus give insight into the scales at which beta diversity might be higher or lower.

A key difference between these two approaches is that the distance-decay relationship is often used to describe directional turnover in species composition, and therefore could be viewed as dissociating aggregate measures of beta diversity into a spatially explicit form. In contrast, diversity partitioning need not be directional, and can give information about variation in species composition among sampling units at different spatial scales. Both of these approaches have advantages for addressing particular kinds of research questions (Anderson *et al.*, 2011). However, recent work by Steinbauer *et al.* (2012) highlighted an important limitation of the distance-decay approach when varying the grain or extent of sampling. Specifically, they showed in model simulations with constant extent of study area, but increasing sample-unit size, that a low slope of the distance-decay relationship may be found in contrasting situations of either very small sample-unit size or very large sample-unit size. When sample-unit size is very small (relative to the study area), even neighbouring sampling units may be very dissimilar due to high variability in species occupancies, resulting in low decay in space. Meanwhile, when sample-unit size is very large, there can be high similarity even between very distant sampling units due to an increased chance of detecting species far from their spatial optima, thus resulting once again in low apparent decay in space (but for very different reasons) (Steinbauer *et al.*, 2012).

Given these considerations, the slope of the distance-decay function and the aggregate beta measures obtained from diversity partitioning are not necessarily going to be telling the same story. As Steinbauer *et al.* (2012) point out, the current spatially explicit approaches used in distance-decay functions are not robust enough to generalize across spatial scales.

In this paper, we take a diversity-partitioning approach to scaling and focus on the interacting effects of grain and extent on aggregate measures of beta diversity. We explore different approaches to conceptualizing the effects of spatial scale on beta diversity, interpreted from 'fixed' and 'varying' perspectives of spatial grain and extent, and discuss the implications of these for understanding variation among communities of different organisms, and for targeting conservation management at different spatial scales.

THE IMPORTANCE OF SCALE

Any putative scaling relationship will be intimately dependent on the spatial scales that are set, or observed, for both alpha and gamma diversity. Absolute scales at which alpha and gamma diversity should be measured have proven elusive. This is partly because ecologists have widely varying objectives in addressing different research questions, and partly because species perceive and respond to the world at widely varying spatial scales (Wiens, 1989; Palmer & White, 1994). Consequently, alpha diversity is typically defined as the base sampling unit at a particular 'site' (often representing the spatial grain of the study), while gamma diversity is defined as the sampling area that is the aggregate of all sampling units (often representing the spatial extent of the study). These choices of spatial grain and extent of sampling are (or at least should be) influenced by the biology of the particular taxon of interest, commonly the size or presumed dispersal capacity. For example, bacterial (Martiny *et al.*, 2011) and soil faunal communities (Nielsen *et al.*, 2010) are often quantified in sampling units of square centimetres, arthropod communities in sampling units of square metres (Kaspari *et al.*, 2010) and mammal communities in sampling units of square kilometres (Svenning *et al.*, 2011). In practice, there is also a strong tendency for spatial grain and extent to be positively correlated (covarying across studies). This is because ecologists often aim to select a scale of field sampling that reflects the biology of the organisms being studied. Of course, ecological studies use a variety of data in addition to the direct sampling mentioned above. This includes checklists and atlases of species occurrences, which will also affect the spatial grain of the sampling units (Hortal, 2008).

It is tempting to see the choices made in the selection of spatial grain and extent as constraints on our ability to measure and interpret beta diversity. Indeed, this problem was highlighted by Nekola & White (1999), and also in the recent modelling study by Steinbauer *et al.* (2012), who suggested that the ecological mechanisms driving variation in distance-decay relationships may potentially be overshadowed by the effects of sampling at different spatial grains or study extents. For these reasons, a thorough understanding of the ways in which spatial grain and extent might affect observed patterns of beta diversity is critical for its proper interpretation. We suggest that a 'spatial window' of observation, defined by the spatial grain of sampling units and the spatial extent of the study area, is an appealing and informative prerequisite for developing any general model of the scaling of beta diversity. Our impression is that a 'spatial window' of observation is implicit in most (if not all) previous studies of beta diversity, but has not been formalized explicitly into a model of spatial scaling.

In general terms, there are three ways in which this spatial window might vary, depending on the objectives of the study and the research questions being addressed. First, one might hold spatial grain constant while increasing spatial extent (Fig. 1a). This idea underpins the species–area relationship, and might be used in the partitioning of species diversity for the same taxa across geographic scales (Gering *et al.*, 2003). Second, one might hold spatial extent constant while varying spatial grain (Fig. 1b), such as might occur when comparing samples of different taxa sampled at different scales but within the same geographic area. Third, one might vary both spatial grain and extent in the generalized case of a 'sliding window', such as when comparing samples of different taxa taken at various spatial scales in different geographic areas (Fig. 1c).
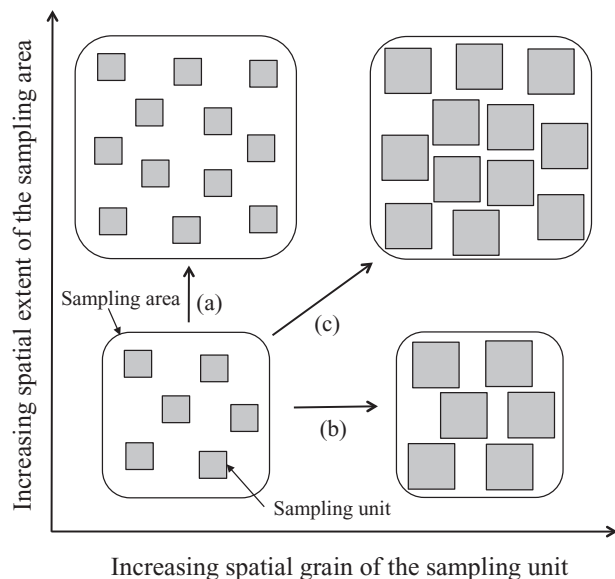
Figure 1 Interpretation of scale dependence in ecological phenomena depends sensitively on how the spatial grain of sampling units and the spatial extent of the sampling area are defined and scaled (after Anderson *et al.*, 2011). The ways in which spatial grain and extent may scale include (a) fixing the spatial grain of the sampling unit and varying the spatial extent of the sampling area, (b) fixing extent and varying the spatial grain of the sampling units, or (c) varying both spatial grain and extent together, giving a 'sliding window' of spatial observation.

A GENERAL MODEL FOR THE SCALING OF BETA DIVERSITY

Mechanistically, variation in diversity at local, regional or global scales is typically ascribed to differing processes operating at different spatial scales (Table 1). These mechanisms can help inform our a priori expectations for how beta diversity might vary among sampling units drawn at each of these scales. In some cases, these expectations have been shown to coincide with a triphasic form of the species–area relationship (Rosenzweig, 1995), which we use as a starting point for discussion on the scaling of beta diversity (but note that our conclusions are not dependent on the specific form that the species–area relationship might take). Typically, species richness increases rapidly at local scales as new sampling units are incorporated, due to high variation in stochastic species occupancy patterns among sites, and deterministic variation in species responses to habitat heterogeneity (Table 1). Beta diversity might therefore be expected to be high among sampling units drawn from within local areas. At regional scales, species richness increases more slowly as fewer new species are encountered relative to the regional pool. Consequently, beta diversity might be lower among sampling units at regional scales, and the rate of increase from local scales might slow. At large global scales, species richness increases again as new species are encountered across biogeographic regions with distinct geological and evolutionary histories (Table 1). Therefore, beta diversity might be higher among sampling units drawn from different continents than among sampling units drawn from within a single region.

It is important to note that the 'beta diversity' we refer to here should not be considered synonymous with the rate of change in alpha diversity across scales. Ideally, models of the spatial scaling of beta diversity should reflect compositional dissimilarity that is statistically independent of the 'true' number of communities sampled (N) and of species richness, as these two variables are likely to change with spatial grain and extent. Whittaker's beta diversity, calculated as $\beta_W = \gamma/\alpha$, is relatively insensitive to species richness but not to community number (Jost, 2007; Baselga, 2010a). Thus, it is important to consider an appropriate normalized measure of differentiation to take variation in the number of communities, or sampling units, into account. Such a measure is one minus the multiple-site Sørensen index (Baselga, 2010b; Chao *et al.*, 2012). This can be interpreted as the

Table 1 A variety of different occupancy, bionomic and biogeographic factors are suggested to drive beta diversity at different spatial scales (Whittaker *et al.*, 2001; Ricklefs, 2004; Hortal *et al.*, 2010).

Spatial scales	Scale of beta diversity	Examples of environmental factors	Examples of organismal factors
Local < 10^6 m^2	Heterogeneity within and between habitat patches	Habitat composition and structure, soils, disturbance	Stochastic occupancy, species interactions, resource specificity, niche requirements
Regional 10^6–10^{10} m^2	Differences in communities across landscapes and large geographic areas within continents	Topology, altitude, discontinuous habitat, latitudinal gradients in productivity and climate, energy dynamics	Dispersal limitation, trophic position, range size, meta-community dynamics
Global > 10^{10} m^2	Variation in evolutionary history across biogeographic regions	Isolation by mountain ranges, continental isolation, plate tectonics	Speciation–extinction events, higher taxon replacement

average among-sample dissimilarity at the specified scale, rather than an overall aggregate measure, and is useful to consider when comparing across taxa or regions with varying levels of richness and community number (Chao *et al.*, 2012).

We contrast these two measures of beta diversity, Whittaker's beta (β_W) versus one minus the multiple-site Sørensen index ($\beta_{Sør}$), in our proposed scaling curves below to highlight the critical importance of proper consideration of both community number and species richness. We adopt the approach of Chao *et al.* (2012) in developing our conceptual scaling curves on the theoretical assumption that N represents the number of 'true' communities with 'true' community parameters of species richness and relative abundances (Chao *et al.*, 2012). We recognize that when scaling curves are constructed from empirical samples, as will be necessary in practice, then the number of sampling units will often incompletely represent the 'true' number of communities, and will require standardization by rarefaction or extrapolation (Colwell *et al.*, 2012). This must be considered prior to the calculation of a normalized differentiation measure, such as one minus the multiple-site Sørensen index (Chao *et al.*, 2012), and will improve comparability of beta-diversity values across different studies.

We combine the 'spatial window' concepts introduced in Fig. 1 with the putative mechanisms suggested to operate at different spatial scales described in Table 1, and propose a series of conceptually different forms of the beta-diversity scaling relationship, depending on whether one takes a 'fixed' or 'varying' perspective of spatial grain and extent (Fig. 2). We suggest that the form of these relationships is unlikely to be linear given the ecological mechanisms operating across local to global scales (Table 1), and might well be logistic in form. Here, we illustrate our arguments with a logistic form of the relationship (Fig. 2), but similar arguments could be made with exponential, logarithmic or even linear relationships.

The scaling relationships will also vary with the measure of beta diversity selected. First, we describe potential scaling curves using an aggregate measure of Whittaker's multiplicative beta diversity. If spatial grain is fixed and spatial extent is allowed to increase, then beta diversity will naturally increase monotonically (Figs 1a & 2a). Alternatively, if spatial extent is fixed and grain is allowed to vary, then beta diversity might be expected to decrease monotonically (Figs 1b & 2b). That is, larger sample-unit areas will capture a larger portion of the community, and similarity between sampling units will increase. If both grain and extent are allowed to vary across spatial scales (a 'sliding window'), then beta diversity might be expected to follow a concave parabolic scaling relationship (Figs 1c & 2c), wherein dissimilarity among sampling units is higher at local and global scales, but lower at regional scales.

The Whittaker's beta scaling relationships, however, do not account for differences in the numbers of sampling units that are likely to occur at different spatial scales. At a comprehensive level of sampling, the number of sampling units will intrinsically decline as spatial grain increases, but increase as spatial extent increases. This will have a dramatic effect on the average 'per

sample' differentiation indicated by one minus the multiple-site Sørensen index. Thus, when spatial grain is small and spatial extent is large, very different values of beta diversity will be indicated by Whittaker's beta compared with the multiple-site Sørensen index. We therefore show three additional curves indicating the likely relationships observed for a normalized differentiation measure such as one minus the multiple-site Sørensen index. What is immediately clear when using this type of average among-sample dissimilarity measure of beta diversity is that the curves will exhibit the opposite scaling relationships to that of Whittaker's beta diversity when either grain is fixed and extent varies (Fig. 2d) or grain varies and extent is fixed (Fig. 2e). Moreover, when extent is fixed at a large spatial scale, the increase in spatial grain is most likely to produce curves that approximate an exponential rather than logistic form (see dashed curves in Fig. 2d, e). This implies that the shape of the scaling curves calculated from a normalized differentiation measure is unlikely to be the symmetrical opposite of its equivalent calculated from Whittaker's beta.

We reiterate that the logistic scaling relationship illustrated here is based on generalized assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however, may not hold in all cases, and may not necessarily result in logistic beta scaling curves in all cases (particularly when using average among-sample dissimilarity measures of beta). We suggest that actual empirical scaling curves of beta diversity are likely to vary from simple linear to complex logistic relationships, depending on the range of spatial scales considered, the structure of the sampling design, the measure of beta diversity used and the taxon or biogeographic areas being examined. Importantly, all underlying scaling assumptions for beta diversity appear to produce similar concave curves when grain and extent are allowed to co-vary using our 'sliding window' perspective (Fig. 2c, f).

The three scaling approaches using the multiple-site Sørensen dissimilarity index outlined above (Fig. 2d–f) can be used to build a three-dimensional surface that shows the interactive effects of grain and extent on beta diversity across the full range of spatial scales (Fig. 3). Here, spatial grain and extent form the horizontal *x*- and *y*-axes, and beta diversity forms the vertical *z*-axis (Fig. 3). At the extremes, as either grain or extent tend to zero, then beta diversity will be logically undefined. Similarly, when grain equals extent, then beta diversity must be zero, as no differentiation among sampling units is possible. Between these logical bounds, we interpolate the remainder of the three-dimensional surface based on the representation of Fig. 2(d)–(f) as two-dimensional vertical 'slices' through the three-dimensional surface. An equivalent (but inversely shaped) response surface could be represented for Whittaker's beta diversity. In essence, this reflects a general form of the beta scaling relationship that might be expected for different study designs aimed at examining community turnover of different kinds of organisms, such as plants (Kraft *et al.*, 2011), vertebrates (Svenning *et al.*, 2011) or microbes (Martiny *et al.*, 2011) along various geographical or environmental gradients. The value of a more general conceptual model for the spatial scaling of beta diversity will be to synthesize across these disparate studies.
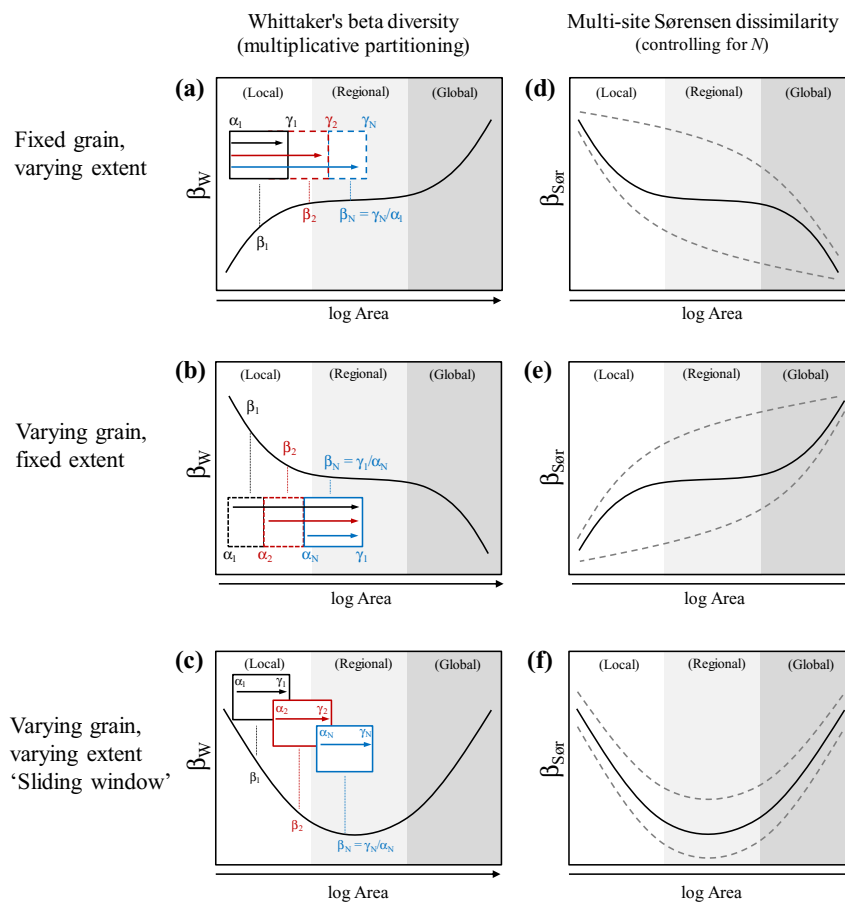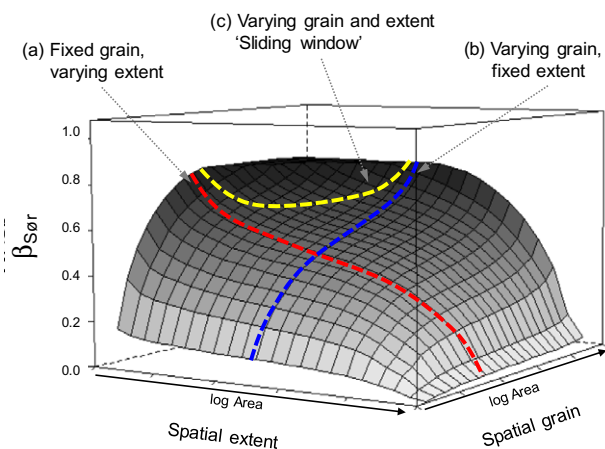
Figure 2 Conceptual approaches to the spatial scaling of beta diversity can be derived from the interaction between sampling grain and study extent, which define the 'spatial window' of observation. The spatial grain of sampling units will define the scale of alpha diversity, and the spatial extent of a study will define the scale of gamma diversity. However, different measures of beta diversity will produce different scaling curves. For a purely aggregate measure such as Whittaker's multiplicative beta ($\beta_W = \gamma/\alpha$), then beta diversity will: (a) increase monotonically if the spatial scale of alpha diversity is fixed but the scale of gamma diversity is allowed to vary; (b) decrease monotonically if the spatial scale of gamma diversity is fixed, but the scale of alpha diversity is allowed to vary; and (c) exhibit a concave parabolic curve if the spatial scales of both alpha and gamma vary together (a 'sliding window'). Aggregate measures of beta can be confounded by the number of sampling sites (N) compared, which intrinsically decline as spatial grain increases but increase as spatial extent increases. A normalized measure of beta that controls for N, such as one minus the multiple-site Sørensen similarity index (β_{Sor}), will produce curves in the opposite direction to Whittaker's beta diversity when either (d) grain or (e) extent is fixed, representing the change in average dissimilarity among sampling units at that scale. The logistic scaling relationship illustrated here is based on generalized assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however, may not hold in all cases, and we suggest that actual empirical scaling curves of beta diversity are likely to vary from simple linear to complex logistic relationships (dashed lines in d–f), depending on the range of spatial scales considered, the structure of the sampling design, the measure of beta diversity and the taxon or biogeographic areas being examined. Importantly, both measures of beta diversity will produce the same concave curve when grain and extent are allowed to covary using our 'sliding window' perspective (c) and (f).

VARIATION IN THE SCALING OF BETA DIVERSITY ACROSS TAXA

Few studies on beta diversity have focused on more than one taxon (Ferrier *et al.*, 2004; Qian & Ricklefs, 2012). This has limited our appreciation of the importance of variation in the scaling of beta diversity across multiple and distinct taxa within and between ecological communities. There are few studies that explicitly compare patterns of beta diversity or endemism across disparate taxa, but evidence gained thus far suggests that divergent patterns exist. This may be because certain traits of organ-isms affect how they perceive and respond to their environment (Wiens, 1989) and how they are spatially distributed (Finlay *et al.*, 2006). Therefore, strong differences in trait complexes among different taxa, such as body size, niche width and dispersal ability, are likely to strongly influence their response to spatial heterogeneity in the environment (Wiens, 1989; Nekola & White, 1999; Soininen *et al.*, 2007). For this reason, it is not surprising that studies have shown that species of large-bodied vertebrate taxa, for example, are often poor surrogates for species richness or endemicity of other taxa (Ferrier *et al.*, 2004; Schuldt & Assmann, 2010).

(a) Fixed grain, varying extent

(c) Varying grain and extent 'Sliding window'

(b) Varying grain, fixed extent

Figure 3 A general conceptual model for the spatial scaling of beta diversity. The three-dimensional surface shows schematically how varying spatial scales of sampling grain and study extent might influence beta diversity. Here, 'beta diversity' is depicted on the vertical axis as one minus the multiple-site Sørensen index (Baselga, 2010b; Chao *et al.*, 2012), but alternative scaling relationships could be depicted for Whittaker's beta (Whittaker, 1960), the effective number of compositionally dissimilar sampling units (Tuomisto, 2010a) or other metrics. The surface interpolates between three two-dimensional 'slices' that represent conceptually different forms of the beta scaling relationship, depending on whether (a) grain is fixed and extent is allowed to vary, (b) extent is fixed and grain is allowed to vary or (c) grain and extent are allowed to vary together in the sense of a 'sliding window' of spatial observation.

Regardless of which groups of organisms are compared, the scaling of beta diversity will not only be dependent on the spatial grain and extent of studies but also on the traits of organisms being studied and the environmental properties of the study environment (see Table 1). These ideas are also reflected in the 'everything is everywhere, but the environment selects' hypothesis, a topic of particular interest among microbial ecologists (Fontaneto, 2011). This debate centres on the relative roles of dispersal versus environmental selection in determining compositional variation through space, and thus levels of beta diversity at different spatial scales (Martiny *et al.*, 2011). However, it also has broader implications for our understanding of the interaction between organism traits and geographic scale. For example, if we consider geographic range size as a surrogate for dispersal, and niche width as a surrogate for environmental selection, there are situations in which different taxa will display different levels of beta diversity. For example, host-specific parasites of large ungulates might have a narrow niche but a large geographic range size, whereas freshwater snails might have both a narrow niche and a small geographic range. In contrast, a generalist herbivore such as a locust will have both a broad niche and large geographic range. But how do these different factors influence the shape of the scaling relationship for beta diversity?

The wide divergence in key ecological traits between taxa suggests that a single idealized form of the beta-diversity scaling relationship will not be appropriate for all taxa. We outline three qualitative predictions that stem from our generalized form of the beta-diversity scaling relationship, and explore how three key traits – body size, resource use specialization and dispersal capacity, might affect beta diversity at different spatial scales.

First, some groups of very small-bodied organisms, such as bacteria or protists, and to some extent insects, are vastly more numerous, diverse and compositionally heterogeneous than plants or vertebrates. Thus, a general scaling curve might change to show higher absolute beta diversity of communities of small organisms across the entire continuum of spatial scale relative to large-bodied organisms (prediction 1). Bacteria are several orders of magnitude smaller than insects, however, and consequently are small enough to be passively dispersed by air currents, for example. This means that some microbes actually have widespread distributions (Fontaneto, 2011), and even within groups of small organisms there may be variation in potential beta-diversity scaling curves Similarly, some migratory butterflies move hundreds of kilometres (Brower, 1961), and small insects are among the first organisms to colonize newly created volcanic islands (New, 2008). Size per se may therefore not necessarily predict dispersal capacity or range size, and therefore compositional turnover at different spatial scales.

Second, organisms will display very different resource use specialization, and thus respond to environmental heterogeneity at different spatial scales. For example, some generalist birds may be able to persist in a wide variety of environments. Conversely, some arthropod groups will have very narrow resource use specialization and track environmental gradients at very fine spatial scales (Kaspari *et al.*, 2010; Nielsen *et al.*, 2010). Thus, organisms with narrower resource specialization will tend to have greater heterogeneity of occurrence at a given scale than organisms with wide resource use, such that a relatively small increase in the area sampled will result in a relatively rapid accumulation of new species. Thus, for organisms with wide resource use, a general scaling curve might change to show lower beta-diversity values among fine-grained sampling units (prediction 2).

Third, dispersal capacity will affect the ability of organisms to colonize suitable environments. Taxa with low average rates of dispersal might be expected to show lower average geographic range sizes and higher rates of local endemism, resulting in higher rates of species turnover at local to regional scales (Qian, 2009; Baselga *et al.*, 2012). For communities with a high proportion of dispersal-limited species, a general scaling curve might therefore be expected to show higher beta-diversity values at small spatial scales (prediction 3).

In reality, there is strong covariance in traits across phylogenetic lineages (Harvey & Pagel, 1991), and we would expect taxa with distinct suites of size, dispersal or resource specialization traits to produce different relative forms of the beta scaling relationship. It might be generalized, for example, that scaling relationships for some groups of organisms with small body size, narrow resource preference and low dispersal capacity will be quite different than for large, dispersive generalist species. We expect that the effect of these types of trait differences on the

precise form of the beta-diversity scaling relationship will be fertile ground for further empirical testing.

IMPLICATIONS

Our perspective on the spatial scaling of beta diversity will have important implications in many areas of ecology, including: (i) the linking of macroecology with phylogeography and ecogenomics, (ii) the design of new studies to understand community assembly at different scales, and (iii) the conceptual underpinning of multiscale biodiversity management.

First, dramatic reductions in the cost of gene sequencing are enabling much finer-grained assessment of microbial biodiversity across regions than ever before (Poole *et al.*, 2012). This has broad implications for the integration of emerging fields, such as ecogenomics, with traditional macroecological studies. In the near future, we can envisage this filling a significant gap in the incorporation of fine-grained empirical data into macroecological studies over large spatial extents (Beck *et al.*, 2012). Such integration may have further implications for phylogeography, and could provide new insights into processes driving community differentiation and endemism through space and time (Schmidt *et al.*, 2011).

Second, it is well established that different factors affect community assembly at different scales. For example, climate and historical factors can act as large-scale filters, whereas habitat structure and dispersal can act as local filters on community assembly (see Table 1). Our 'sliding window' perspective on spatial grain and extent may provide a useful framework to design new studies, or meta-analysis of pre-existing datasets, to examine the relative effects of multiple filters on community assembly, and thus beta diversity, across multiple scales (Rajaniemi *et al.*, 2006; Wang *et al.*, 2009).

Third, if beta-diversity scaling relationships vary widely across disparate organisms, then conservation strategies will need to focus more explicitly on the requirements of multiple taxa at multiple spatial scales to prevent the loss of species (Lindenmayer & Franklin, 2002). Any credible plan for biodiversity conservation must maintain beta diversity (and the processes that shape it) across the full range of taxa and spatial scales. The only way to achieve this will be through multiscaled conservation approaches (Lindenmayer & Franklin, 2002). At present, conservation management is generally planned at 'regional' scales (Ferrier *et al.*, 2004) and implemented for a small subset of biodiversity (typically vertebrates and plants) at 'local' scales (Bestelmeyer *et al.*, 2003). These local scales are almost invariably defined at human-perceived spatial grains within landscapes (e.g. field or farm scales), which do not match the spatial scales of perception of the majority of organisms that are much smaller in size (Manning *et al.*, 2004). Although there are some examples of reserves being created for threatened insect species (Brereton *et al.*, 2008; Watts & Thornburrow, 2009), and some consideration of insects in conservation planning at multiple scales (Cabeza *et al.*, 2010), there are limited examples of active management that considers the fine-grained niche requirements of insect species within landscapes. Some examples where this has occurred include the enhancement of food resources within a forestry context (Gibb *et al.*, 2006), addition of microhabitat complexity within a restoration context (Barton *et al.*, 2011) or the planting of field margins in agricultural contexts (Pywell *et al.*, 2011). By contrast, most management interventions at larger scales, such as tree plantings, may enhance only the perceived 'quality' of habitat for a subset of vertebrate species at landscape scales (Cunningham *et al.*, 2007). This may have limited or no effect on some groups of organisms that perceive and respond to plant composition at finer spatial scales (Tylianakis *et al.*, 2006; Barton *et al.*, 2010). This is not to say that management intervention at landscape scales is unimportant. Rather, interventions leading to an improvement in fine-scale habitat conditions within sites that are subsets of the larger landscape are more likely to affect the composition of diverse arthropod assemblages than landscape-scale interventions. In this sense, management interventions at different spatial scales should be seen as complementary, as they affect different suites of taxa.

CONCLUSIONS

By establishing some expectations for how beta diversity varies across spatial scales, the critical role that sampling and study design plays and how these patterns might vary with organism traits, we hope to stimulate the development of a more general framework for testing the processes structuring communities and ecosystems. This has broad implications for the integration of emerging fields, such as ecogenomics with traditional macroecological studies. We suggest that there are also significant opportunities for conservation managers to make biodiversity gains if the spatial scaling of beta diversity is properly considered across different taxa with contrasting traits, and incorporated into management actions at multiple spatial scales. High habitat specificity and poor dispersal ability are characteristics that favour speciation and compositional turnover, but which are not typical of the charismatic vertebrates for which many reserve systems are designed. We argue that a greater understanding of the spatial scaling of beta diversity will be crucial for improving conservation theory and practice. Exploring the conceptual underpinnings of the spatial scaling of beta diversity will enable a deeper integration of biodiversity phenomena at vastly different scales and across distinct groups of organisms.

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BIOSKETCH

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P.B., S.C. and R.D. conceived the main ideas, and all authors contributed to their development. P.B. and R.D. wrote the paper, with comments from all authors.

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