3

4   The spatial scaling of beta diversity

5

6   Philip S. Barton [1,2,3,*], Saul A. Cunningham [3], Adrian D. Manning [1], Heloise Gibb [4], David B.

7   Lindenmayer [1,2], Raphael K. Didham [5,6]

8

9   [1] Fenner School of Environment and Society, The Australian National University, Canberra,

10   Australian Capital Territory, 0200, Australia.

11   [2] ARC Centre of Excellence for Environmental Decisions and National Environmental Research

12   Program, The Australian National University, Canberra, Australian Capital Territory, 0200,

13   Australia.

14   [3] CSIRO Ecosystem Sciences, Canberra, Australian Capital Territory, 2601, Australia.

15   [4] Department of Zoology, La Trobe University, Bundoora, Victoria, 3086, Australia.

16   [5] CSIRO Ecosystem Sciences, Floreat, Western Australia, 6014, Australia.

17   [6] School of Animal Biology, The University of Western Australia, Perth, Western Australia, 6009,

18   Australia.

19   *Corresponding author: Email: philip.barton@anu.edu.au

20

21

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 conceptualise 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 eco-genomic data with large-scale macroecological studies, as well as for guiding appropriate management responses to threats to biodiversity operating at different spatial scales.

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, 2010b; Tuomisto, 2010a; 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 grain and extent (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 conceptualise 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 parameterise 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 *et al.* 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-

4

96　unit size or very large sample-unit size. When sample-unit size is very small (relative to the study

97　area), even neighbouring sampling units may be very dissimilar due to high variability in species

98　occupancies, resulting in low decay in space. Meanwhile, when sample-unit size is very large, there

99　can be high similarity even between very distant sampling units due to an increased chance of

100　detecting species far from their spatial optima, thus resulting once again in low apparent decay in

101　space (but for very different reasons) (Steinbauer *et al.* 2012).

102　　　Given these considerations, the slope of the distance-decay function and the aggregate beta

103　measures obtained from diversity partitioning are not necessarily going to be telling the same story.

104　As Steinbauer *et al.* (2012) point out, the current spatially-explicit approaches used in distance-

105　decay functions are not robust enough to generalise across spatial scales.

106　　　In this paper, we take a diversity-partitioning approach to scaling and focus on the

107　interacting effects of grain and extent on aggregate measures of beta diversity. We explore different

108　approaches to conceptualising the effects of spatial scale on beta diversity, interpreted from 'fixed'

109　and 'varying' perspectives of spatial grain and extent, and discuss the implications of these for

110　understanding variation among communities of different organisms, and for targeting conservation

111　management at different spatial scales.

112

113　**THE IMPORTANCE OF SCALE**

114　Any putative scaling relationship will be intimately dependent on the spatial scales that are set, or

115　observed, for both alpha and gamma diversity. Absolute scales at which alpha and gamma diversity

116　should be measured have proven elusive. This is partly because ecologists have widely varying

117　objectives in addressing different research questions, and partly because species perceive and

118　respond to the world at widely varying spatial scales (Wiens, 1989; Palmer & White, 1994).

119　Consequently, alpha diversity is typically defined as the base sampling unit at a particular 'site'

120　(often representing the spatial grain of the study), while gamma diversity is defined as the sampling

121　area that is the aggregate of all sampling units (often representing the spatial extent of the study).

122   These choices of spatial grain and extent of sampling are (or at least should be) influenced by the

123   biology of the particular taxon of interest, commonly the size or presumed dispersal capacity. For

124   example, bacterial (Martiny *et al.*, 2011) and soil faunal communities (Nielsen *et al.*, 2010) are

125   often quantified in sampling units of square centimetres, arthropod communities in sampling units

126   of square metres (Kaspari *et al.*, 2010), and mammal communities in sampling units of square

127   kilometres (Svenning *et al.*, 2011). In practice, there is also a strong tendency for spatial grain and

128   extent to be positively correlated (co-varying across studies). This is because ecologists often aim to

129   select a scale of field sampling that reflects the biology of the organisms being studied. Of course,

130   ecological studies use a variety of data in addition to the direct sampling mentioned above. This

131   includes checklists and atlases of species occurrences, which also will affect the spatial grain of the

132   sampling units (Hortal, 2008).

133   It is tempting to see the choices made in the selection of spatial grain and extent as

134   constraints on our ability to measure and interpret beta diversity. Indeed, this problem was

135   highlighted by Nekola & White (1999), and also in the recent modelling study by Steinbauer *et al.*

136   (2012), who suggested that the ecological mechanisms driving variation in distance-decay

137   relationships may potentially be overshadowed by the effects of sampling at different spatial grains

138   or study extents. For these reasons, a thorough understanding of the ways in which spatial grain and

139   extent might affect observed patterns of beta diversity is critical for its proper interpretation. We

140   suggest that a 'spatial window' of observation, defined by the spatial grain of sampling units and

141   the spatial extent of the study area, is an appealing and informative prerequisite for developing any

142   general model of the scaling of beta diversity. Our impression is that a 'spatial window' of

143   observation is implicit in most (if not all) previous beta diversity studies, but has not been

144   formalised explicitly into a model of spatial scaling.

145   In general terms, there are three ways in which this spatial window might vary, depending

146   on the objectives of the study and the research questions being addressed. First, one might hold

147   spatial grain constant while increasing spatial extent (Fig. 1a). This idea underpins the species-area

148 relationship, and might be used in the partitioning of species diversity for the same taxa across

149 geographic scales (Gering *et al.*, 2003). Second, one might hold spatial extent constant while

150 varying spatial grain (Fig. 1b), such as might occur when comparing samples of different taxa

151 sampled at different scales but within the same geographic area. Third, one might vary both spatial

152 grain and extent in the generalised case of a 'sliding window', such as when comparing samples of

153 different taxa taken at various spatial scales in different geographic areas (Fig. 1c).

154

155 **A GENERAL MODEL FOR THE SCALING OF BETA DIVERSITY**

156 Mechanistically, variation in diversity at local, regional or global scales is typically ascribed to

157 differing processes operating at different spatial scales (Table 1). These mechanisms can help

158 inform our *a priori* expectations for how beta diversity might vary among sampling units drawn at

159 each of these scales. In some cases, these expectations have been shown to coincide with a triphasic

160 form of the species-area relationship (Rosenzweig, 1995), which we use as a starting point for

161 discussion on the scaling of beta diversity (but note that our conclusions are not dependent on the

162 specific form that the SAR might take). Typically, species richness increases rapidly at local scales

163 as new sampling units are incorporated, due to high variation in stochastic species occupancy

164 patterns among sites, and deterministic variation in species responses to habitat heterogeneity

165 (Table 1). Beta diversity might therefore be expected to be high among sampling units drawn from

166 within local areas. At regional scales, species richness increases more slowly as fewer new species

167 are encountered relative to the regional pool. Consequently, beta diversity might be lower among

168 sampling units at regional scales, and the rate of increase from local scales might slow. At large

169 global scales, species richness increases again as new species are encountered across biogeographic

170 regions with distinct geological and evolutionary histories (Table 1). Therefore, beta diversity might

171 be higher among sampling units drawn from different continents than among sampling units drawn

172 from within a single region.

173   It is important to note that the 'beta diversity' we refer to here should not be considered

174   synonymous with the rate of change in alpha diversity across scales. Ideally, models of the spatial

175   scaling of beta diversity should reflect compositional dissimilarity that is statistically independent of

176   the 'true' number of communities sampled (N) and of species richness, as these two variables are

177   likely to change with spatial grain and extent. Whittaker's beta diversity, calculated as $\beta_W = \gamma/\alpha$, is

178   relatively insensitive to species richness but not to community number (Jost, 2007; Baselga, 2010a).

179   Thus, it is important to consider an appropriate normalized measure of differentiation to take

180   variation in the number of communities, or sampling units, into account. Such a measure is one

181   minus the multiple-site Sørensen index (Baselga, 2010b; Chao *et al.*, 2012). This can be interpreted

182   as the average among-sample dissimilarity at the specified scale, rather than an overall aggregate

183   measure, and is useful to consider when comparing across taxa or regions with varying levels of

184   richness and community number (Chao *et al.*, 2012).

185   We contrast these two measures of beta diversity, Whittaker's beta (β_W) versus one minus

186   the multiple-site Sørensen index ($\beta_{Sør}$), in our proposed scaling curves below to highlight the critical

187   importance of proper consideration of both community number and species richness. We adopt the

188   approach of Chao *et al.* (2012) in developing our conceptual scaling curves on the theoretical

189   assumption that N represents the number of 'true' communities with 'true' community parameters

190   of species richness and relative abundances (Chao *et al.*, 2012). We recognise that when scaling

191   curves are constructed from empirical samples, as will be necessary in practice, then the number of

192   sampling units will often incompletely represent the 'true' number of communities, and will require

193   standardisation by rarefaction or extrapolation (Colwell *et al.*, 2012). This must be considered prior

194   to the calculation of a normalised differentiation measure, such as one minus the multiple-site

195   Sørensen index (Chao *et al.*, 2012), and will improve comparability of beta diversity values across

196   different studies.

197   We combine the 'spatial window' concepts introduced in Fig 1 with the putative

198   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 normalised 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

225 exhibit the opposite scaling relationships to that of Whittaker's beta diversity when either grain is

226 fixed and extent varies (Fig 2d) or grain varies and extent is fixed (Fig 2e). Moreover, when extent

227 is fixed at a large spatial scale, the increase in spatial grain is most likely to produce curves that

228 approximate an exponential rather than logistic form (see dashed curves in Fig 2d and 2e). This

229 implies that the shape of the scaling curves calculated from a normalised differentiation measure is

230 unlikely to be the symmetrical opposite of its equivalent calculated from Whittaker's beta.

231   We reiterate that the logistic scaling relationship illustrated here is based on generalised

232 assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however,

233 may not hold in all cases, and may not necessarily result in logistic beta scaling curves in all cases

234 (particularly when using average among-sample dissimilarity measures of beta). We suggest that

235 actual empirical scaling curves of beta diversity are likely to vary from simple linear to complex

236 logistic relationships, depending on the range of spatial scales considered, the structure of the

237 sampling design, the measure of beta diversity used, and the taxon or biogeographic areas being

238 examined. Importantly, all underlying scaling assumptions for beta diversity appear to produce

239 similar concave curves when grain and extent are allowed to co-vary using our 'sliding window'

240 perspective (Fig 2c and 2f).

241   The three scaling approaches using the multiple-site Sørensen dissimilarity index outlined

242 above (Fig 2 d, e, f) can be used to build a three-dimensional surface that shows the interactive

243 effects of grain and extent on beta diversity across the full range of spatial scales (Fig. 3). Here,

244 spatial grain and extent form the horizontal x- and y- axes, and beta diversity forms the vertical z-

245 axis (Fig 3). At the extremes, as either grain or extent tend to zero, then beta will be logically

246 undefined. Similarly, when grain equals extent, then beta diversity must be zero, as no

247 differentiation among sampling units is possible. Between these logical bounds, we interpolate the

248 remainder of the 3D surface based on the representation of Figures 2 d, e, and f as two-dimensional

249 vertical 'slices' through the three-dimensional surface. An equivalent (but inversely-shaped)

250 response surface could be represented for Whittaker's beta diversity. In essence, this reflects a

251   general form of the beta scaling relationship that might be expected for different study designs

252   aimed at examining community turnover of different kinds of organisms, such as plants (Kraft *et*

253   *al.*, 2011), vertebrates (Svenning *et al.*, 2011), or microbes (Martiny *et al.*, 2011) along various

254   geographical or environmental gradients. The value of a more general conceptual model for the

255   spatial scaling of beta diversity will be to synthesise across these disparate studies.

256

257   **VARIATION IN THE SCALING OF BETA DIVERSITY ACROSS TAXA**

258   Few studies on beta diversity have focused on more than one taxon (Ferrier *et al.*, 2004; Qian &

259   Ricklefs, 2012). This has limited our appreciation of the importance of variation in the scaling of

260   beta diversity across multiple and distinct taxa within and between ecological communities. There

261   are few studies that explicitly compare patterns of beta diversity or endemism across disparate taxa,

262   but evidence gained thus far suggests that divergent patterns exist. This may be because certain

263   traits of organisms affect how they perceive and respond to their environment (Wiens, 1989) and

264   how they are spatially distributed (Finlay *et al.*, 2006). Therefore, strong differences in trait

265   complexes among different taxa, such as body size, niche width, and dispersal ability, are likely to

266   strongly influence their response to spatial heterogeneity in the environment (Wiens, 1989; Nekola

267   & White, 1999; Soininen *et al.*, 2007). For this reason, it is not surprising that studies have shown

268   that species of large-bodied vertebrate taxa, for example, are often poor surrogates for species

269   richness or endemicity of other taxa (Ferrier *et al.*, 2004; Schuldt & Assmann, 2010).

270   Regardless of which groups of organisms are compared, the scaling of beta diversity will not

271   only be dependent on the spatial grain and extent of studies, but also on the traits of organisms

272   being studied, and the environmental properties of the study environment (see Table 1). These ideas

273   are also reflected in the 'everything is everywhere, but the environment selects' hypothesis, a topic

274   of particular interest among microbial ecologists (Fontaneto, 2011). This debate centres on the

275   relative roles of dispersal versus environmental selection in determining compositional variation

276   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 idealised form of the beta diversity scaling relationship will not be appropriate for all taxa. We outline three qualitative predictions that stem from our generalised form of the beta diversity scaling relationship, and explore how three key traits: (i) body size, (ii) resource use specialisation, and (iii) 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 colonise 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.

303   Second, organisms will display very different resource use specialisation, and thus respond

304   to environmental heterogeneity at different spatial scales. For example, some generalist birds may

305   be able to persist in a wide variety of environments. Conversely, some arthropod groups will have

306   very narrow resource use specialisation and track environmental gradients at very fine spatial scales

307   (Kaspari *et al*., 2010; Nielsen *et al*., 2010). Thus, organisms with narrower resource specialisation

308   will tend to have greater heterogeneity of occurrence at a given scale than organisms with wide

309   resource use, such that a relatively small increase in the area sampled will result in a relatively rapid

310   accumulation of new species. Thus, for organisms with wide resource use, a general scaling curve

311   might change to show lower beta diversity values among fine-grained sampling units (prediction 2).

312   Third, dispersal capacity will affect the ability of organisms to colonise suitable

313   environments. Taxa with low average rates of dispersal might be expected to show lower average

314   geographic range sizes and higher rates of local endemism, resulting in higher rates of species

315   turnover at local to regional scales (Qian, 2009; Baselga *et al.*, 2012). For communities with a high

316   proportion of dispersal limited species, a general scaling curve might therefore be expected to show

317   higher beta diversity values at small spatial scales (prediction 3).

318   In reality, there is strong covariance in traits across phylogenetic lineages (Harvey & Pagel,

319   1991), and we would expect taxa with distinct suites of size, dispersal or resource specialisation

320   traits to produce different relative forms of the beta scaling relationship. It might be generalised, for

321   example, that scaling relationships for some groups of organisms with small body size, narrow

322   resource preference and low dispersal capacity will be quite different than for large, dispersive

323   generalist species. We expect that the effect of these types of trait differences on the precise form of

324   the beta diversity scaling relationship will be fertile ground for further empirical testing.

325

326   **IMPLICATIONS**

327   Our perspective on the spatial scaling of beta diversity will have important implications in many

328   areas of ecology, including (i) the linking of macroecology with phylogeography and ecogenomics,

329 (ii) the design of new studies to understand community assembly at different scales, and (iii) the

330 conceptual underpinning of multi-scale biodiversity management.

331   First, dramatic reductions in the cost of gene sequencing are enabling much finer-grained

332 assessment of microbial biodiversity across regions than ever before (Poole *et al.*, 2012). This has

333 broad implications for the integration of emerging fields, such as ecogenomics, with traditional

334 macroecological studies. In the near future, we can envisage this filling a significant gap in the

335 incorporation of fine-grained empirical data into macroecological studies over large spatial extents

336 (Beck *et al.*, 2012). Such integration may have further implications for phylogeography, and could

337 provide new insights into processes driving community differentiation and endemism through space

338 and time (Schmidt *et al.*, 2011).

339   Second, it is well established that different factors affect community assembly at different

340 scales. For example, climate and historical factors can act as large scale filters, whereas habitat

341 structure and dispersal can act as local filters on community assembly (see Table 1). Our 'sliding

342 window' perspective on spatial grain and extent may provide a useful framework to design new

343 studies, or meta-analysis of pre-existing datasets, to examine the relative effects of multiple filters

344 on community assembly, and thus beta diversity, across multiple scales (Rajaniemi *et al.*, 2006;

345 Wang *et al.*, 2009).

346   Third, if beta diversity scaling relationships vary widely across disparate organisms, then

347 conservation strategies will need to focus more explicitly on the requirements of multiple taxa at

348 multiple spatial scales to prevent the loss of species (Lindenmayer & Franklin, 2002). Any credible

349 plan for biodiversity conservation must maintain beta diversity (and the processes that shape it)

350 across the full range of taxa and spatial scales. The only way to achieve this will be through multi-

351 scaled conservation approaches (Lindenmayer & Franklin, 2002). At present, conservation

352 management is generally planned at 'regional' scales (Ferrier *et al.*, 2004) and implemented for a

353 small subset of biodiversity (typically vertebrates and plants) at 'local' scales (Bestelmeyer *et al.*,

354 2003). These local scales are almost invariably defined at human-perceived spatial grains within

355 landscapes (e.g. field or farm scales), which do not match the spatial scales of perception of the

356 majority of organisms that are much smaller in size (Manning *et al.*, 2004). Although there are

357 some examples of reserves being created for threatened insect species (Brereton *et al.*, 2008; Watts

358 & Thornburrow, 2009), and some consideration of insects in conservation planning at multiple

359 scales (Cabeza *et al.*, 2010), there are limited examples of active management that considers the

360 fine grained niche requirements of insect species within landscapes. Some examples where this has

361 occurred include the enhancement of food resources within a forestry context (Gibb *et al.*, 2006),

362 addition of microhabitat complexity within a restoration context (Barton *et al.*, 2011), or the

363 planting of field margins in agricultural contexts (Pywell *et al.*, 2011). By contrast, most

364 management interventions at larger scales, such as tree plantings, may enhance only the perceived

365 'quality' of habitat for a subset of vertebrates species at landscape scales (Cunningham *et al.*, 2007).

366 This may have limited or no effect on some groups of organisms that perceive and respond to plant

367 composition at finer spatial scales (Tylianakis *et al.*, 2006; Barton *et al.*, 2010). This is not to say

368 that management intervention at landscape scales is unimportant. Rather, interventions leading to an

369 improvement in fine-scale habitat conditions within sites that are subsets of the larger landscape are

370 more likely to affect the composition of diverse arthropod assemblages than landscape-scale

371 interventions. In this sense, management interventions at different spatial scales should be seen as

372 complementary, as they affect different suites of taxa.

373

374 **CONCLUSIONS**

375 By establishing some expectations for how beta diversity varies across spatial scales, the critical

376 role that sampling and study design plays, and how these patterns might vary with organism traits,

377 we hope to stimulate development of a more general framework for testing the processes structuring

378 communities and ecosystems. This has broad implications for the integration of emerging fields,

379 such as ecogenomics with traditional macroecological studies. We suggest there are also significant

380 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 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.

ACKNOWLEDGEMENTS

BIOSKETCH

Philip Barton is a research fellow at the Fenner School of Environment and Society, Australian National University. His research focuses on examining the spatial and temporal drivers of insect, plant and vertebrate community dynamics and its application to ecosystem restoration and biodiversity conservation. PB, SC and RD conceived the main ideas, and all authors contributed to their development. PB and RD wrote the paper, with comments from all authors.

REFERENCES

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C.

407 & Swenson, N. G. (2011) Navigating the multiple meanings of beta diversity: a roadmap for

408 the practicing ecologist. *Ecology Letters*, **14**, 19-28.

409 Barton, P. S., Manning, A. D., Gibb, H., Lindenmayer, D. B. & Cunningham, S. A. (2010) Fine-

410 scale heterogeneity in beetle assemblages under co-occurring *Eucalyptus* in the same

411 subgenus. *Journal of Biogeography*, **37**, 1927-1937.

412 Barton, P. S., Manning, A. D., Gibb, H., Wood, J. T., Lindenmayer, D. B. & Cunningham, S. A.

413 (2011) Experimental reduction of native vertebrate grazing and addition of logs benefit beetle

414 diversity at multiple scales. *Journal of Applied Ecology*, **48**, 943-951.

415 Baselga, A. (2010a) Multiplicative partition of true diversity yields independent alpha and beta

416 components; additive partition does not. *Ecology*, **91**, 1974-1981.

417 Baselga, A. (2010b) Partitioning the turnover and nestedness components of beta diversity. *Global

418 Ecology and Biogeography*, **19**, 134-143.

419 Baselga, A., Lobo, J. M., Svenning, J. C., Aragón, P. & Araújo, M. B. (2012) Dispersal ability

420 modulates the strength of the latitudinal richness gradient in European beetles. *Global

421 Ecology and Biogeography*, in press.

422 Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C.,

423 Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M. & Dormann, C. F. (2012)

424 What's on the horizon for macroecology? *Ecography*, **early view**, doi: 10.1111/j.1600-

425 0587.2012.07364.x.

426 Bestelmeyer, B. T., Miller, J. R. & Wiens, J. A. (2003) Applying species diversity theory to land

427 management. *Ecological Applications*, **13**, 1750-1761.

428 Brereton, T. M., Warren, M. S., Roy, D. B. & Stewart, K. (2008) The changing status of the

429 Chalkhill Blue butterfly Polyommatus coridon in the UK: the impacts of conservation policies

430 and environmental factors. *Journal of Insect Conservation*, **12**, 629-638.

431 Brower, L. P. (1961) Studies on migration of Monarch butterfly.1. Breeding populations of *Danaus

432 plexippus* and *D gilippus berenice* in south central Florida. *Ecology*, **42**, 76-83.

433 Cabeza, M., Arponen, A., Jaattela, L., Kujala, H., Van Teeffelen, A. & Hanski, I. (2010)

434   Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54-63.

435 Chao, A., Chiu, C.-H. & Hsieh, T. C. (2012) Proposing a resolution to debates on diversity

436   partitioning. *Ecology*, **in press**.

437 Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L. & Longino, J. T.

438   (2012) Models and estimators linking individual-based and sample-based rarefaction,

439   extrapolation and comparison of assemblages. *Journal of Plant Ecology*, **5**, 3–21.

440 Cunningham, R. B., Lindenmayer, D. B., Crane, M., Michael, D. & Macgregor, C. (2007) Reptile

441   and arboreal marsupial response to replanted vegetation in agricultural landscapes. *Ecological*

442   *Applications*, **17**, 609-619.

443 Ferrier, S., Powell, G. V. N., Richardson, K. S., Manion, G., Overton, J. M., Allnutt, T. F.,

444   Cameron, S. E., Mantle, K., Burgess, N. D., Faith, D. P., Lamoreux, J. F., Kier, G., Hijmans,

445   R. J., Funk, V. A., Cassis, G. A., Fisher, B. L., Flemons, P., Lees, D., Lovett, J. C. & Van

446   Rompaey, R. (2004) Mapping more of terrestrial biodiversity for global conservation

447   assessment. *Bioscience*, **54**, 1101-1109.

448 Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. a. F., Guegan, J. F.,

449   Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'brien, E. M. & Turner, J. R.

450   G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of*

451   *Biogeography*, **36**, 132-147.

452 Finlay, B. J., Thomas, J. A., Mcgavin, G. C., Fenchel, T. & Clarke, R. T. (2006) Self-similar

453   patterns of nature: insect diversity at local to global scales. *Proceedings of the Royal Society*

454   *B-Biological Sciences*, **273**, 1935-1941.

455 Fontaneto, D. (2011) *Biogeography of micro-organisms. Is everything small everywhere?*, edn.

456   Cambridge University Press.

457 Gering, J. C., Crist, T. O. & Veech, J. A. (2003) Additive partitioning of species diversity across

458   multiple spatial scales: Implications for regional conservation of biodiversity. *Conservation*

459   *Biology*, **17**, 488-499.

460 Gibb, H., Hjälten, J., Ball, J. P., Atlegrim, O., Pettersson, R. B., Hilszczanski, J., Johansson, T. &

461   Danell, K. (2006) Effects of landscape composition and substrate availability on saproxylic

462   beetles in boreal forests: a study using experimental logs for monitoring assemblages.

463   *Ecography*, **29**, 191-204.

464 Harvey, P. H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology.*, edn. Oxford

465   University Press, New York, USA.

466 Hortal, J. (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. *Journal of*

467   *Biogeography*, **35**, 1335-1336.

468 Hortal, J., Roura-Pascual, N., Sanders, N. J. & Rahbek, C. (2010) Understanding (insect) species

469   distributions across spatial scales. *Ecography*, **33**, 51-53.

470 Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**,

471   2427-2439.

472 Jurasinski, G., Retzer, V. & Beierkuhnlein, C. (2009) Inventory, differentiation, and proportional

473   diversity: a consistent terminology for quantifying species diversity. *Oecologia*, **159**, 15-26.

474 Kaspari, M., Stevenson, B. S., Shik, J. & Kerekes, J. F. (2010) Scaling community structure: how

475   bacteria, fungi and ant taxocences differentiate along a tropical forest floor. *Ecology*, **91**,

476   2221-2226.

477 Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J.

478   C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L.,

479   Inouye, B. D., Harrison, S. P. & Myers, J. A. (2011) Disentangling the drivers of beta

480   diversity along latitudinal and alevational gradients. *Science*, **333**, 1755-1758.

481 Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple

482   communities. *Oikos*, **76**, 5-13.

483 Lindenmayer, D. B. & Franklin, J. F. (2002) *Conserving forest biodiversity: A comprehensive*

484 *multi-scaled approach.*, edn. Island Press, Washington.

485 Manning, A. D., Lindenmayer, D. B. & Nix, H. A. (2004) Continua and Umwelt: novel

486 perspectives on viewing landscapes. *Oikos*, **104**, 621-628.

487 Martiny, J. B. H., Eisen, J. A., Penn, K., Allison, S. D. & Horner-Devine, M. C. (2011) Drivers of

488 bacterial beta-diversity depend on spatial scale. *Proceedings of the National Academy of*

489 *Sciences of the United States of America*, **108**, 7850-7854.

490 Nekola, J. C. & White, P. S. (1999) The distance decay of similarity in biogeography and ecology.

491 *Journal of Biogeography*, **26**, 867-878.

492 New, T. R. (2008) Insect conservation in early succession on islands: lessons from Surtsey, Iceland,

493 and the Krakatau Archipelago, Indonesia. *Journal of Insect Conservation*, **12**, 307–312.

494 Nielsen, U. N., Osler, G. H. R., Campbell, C. D., Neilson, R., Burslem, D. & Van Der Wal, R.

495 (2010) The enigma of soil animal species diversity revisited: the role of small-scale

496 heterogeneity. *PLoS ONE*, **5 (7)**, e11567.

497 Palmer, M. W. & White, P. S. (1994) Scale dependence and the species-area relationship. *American*

498 *Naturalist*, **144**, 717-740.

499 Poole, A. M., Stouffer, D. B. & Tylianakis, J. M. (2012) 'Ecosystomics': ecology by sequencer.

500 *Trends in Ecology & Evolution*, **27**, 309-310.

501 Pywell, R. F., Meek, W. R., Loxton, R. G., Nowakowski, M., Carvell, C. & Woodcock, B. (2011)

502 Ecological restoration on farmland can drive beneficial functional responses in plant and

503 invertebrate communities. *Agriculture Ecosystems & Environment*, **140**, 62-67.

504 Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America.

505 *Global Ecology and Biogeography*, **18**, 327-332.

506 Qian, H. & Ricklefs, R. E. (2012) Disentangling the effects of geographic distance and

507 environmental dissimilarity on global patterns of species turnover. *Global Ecology and*

508 *Biogeography*, **21**, 341-351.

509   Rajaniemi, T. K., Goldberg, D. E., Turkington, R. & Dyer, A. R. (2006) Quantitative partitioning of

510   regional and local processes shaping regional diversity patterns. *Ecology Letters*, **9**, 121-128.

511   Ricklefs, R. E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology*

512   *Letters*, **7**, 1-15.

513   Rosenzweig, M. L. (1995) *Species diversity in space and time*, edn. Cambridge University Press.

514   Schmidt, S. K., Lynch, R. C., King, A. J., Karki, D., Robeson, M. S., Nagy, L., Williams, M. W.,

515   Mitter, M. S. & Freeman, K. R. (2011) Phylogeography of microbial phototrophs in the dry

516   valleys of the high Himalayas and Antarctica. *Proceedings of the Royal Society B-Biological*

517   *Sciences*, **278**, 702-708.

518   Schuldt, A. & Assmann, T. (2010) Invertebrate diversity and national responsibility for species

519   conservation across Europe - A multi-taxon approach. *Biological Conservation*, **143**, 2747-

520   2756.

521   Soininen, J., Lennon, J. J. & Hillebrand, H. (2007) A multivariate analysis of beta diversity across

522   organisms and environments. *Ecology*, **88**, 2830-2838.

523   Steinbauer, M., Dolos, K., Reineking, B. & Beierkuhnlein, C. (2012) Current measures for distance

524   decay in similarity of species composition are influenced by study extent and grain size.

525   *Global Ecology and Biogeography*, DOI: 10.1111/j.1466-8238.2012.00772.x.

526   Svenning, J. C., Fløjgaard, C. & Baselga, A. (2011) Climate, history and neutrality as drivers of

527   mammal beta diversity in Europe: insights from multiscale deconstruction. *Journal of Animal*

528   *Ecology*, **80**, 393-402.

529   Tuomisto, H. (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1.

530   Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2-22.

531   Tuomisto, H. (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2.

532   Quantifying beta diversity and related phenomena. *Ecography*, **33**, 23-45.

533 Tylianakis, J. M., Klein, A. M., Lozada, T. & Tscharntke, T. (2006) Spatial scale of observation

534   affects alpha, beta and gamma diversity of cavity-nesting bees and wasps across a tropical

535   land-use gradient. *Journal of Biogeography*, **33**, 1295-1304.

536 Veech, J. A. & Crist, T. O. (2010) Toward a unified view of diversity partitioning. *Ecology*, **91**,

537   1988-1992.

538 Wang, X. P., Fang, J. Y., Sanders, N. J., White, P. S. & Tang, Z. Y. (2009) Relative importance of

539   climate vs local factors in shaping the regional patterns of forest plant richness across

540   northeast China. *Ecography*, **32**, 133-142.

541 Watts, C. & Thornburrow, D. (2009) Where have all the weta gone? Results after two decades of

542   transferring a threatened New Zealand giant weta, Deinacrida mahoenui. *Journal of Insect*

543   *Conservation*, **13**, 287-295.

544 Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*

545   *Monographs*, **30**, 279-338.

546 Whittaker, R. J., Willis, K. J. & Field, R. (2001) Scale and species richness: towards a general,

547   hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.

548 Wiens, J. A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.

549

550

551

552 **Table 1**. A variety of different occupancy, bionomic, and biogeographic factors are suggested to

553 drive beta diversity at different spatial scales (Whittaker *et al.*, 2001; Ricklefs, 2004; Hortal *et al.*,

554 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

555

556

557
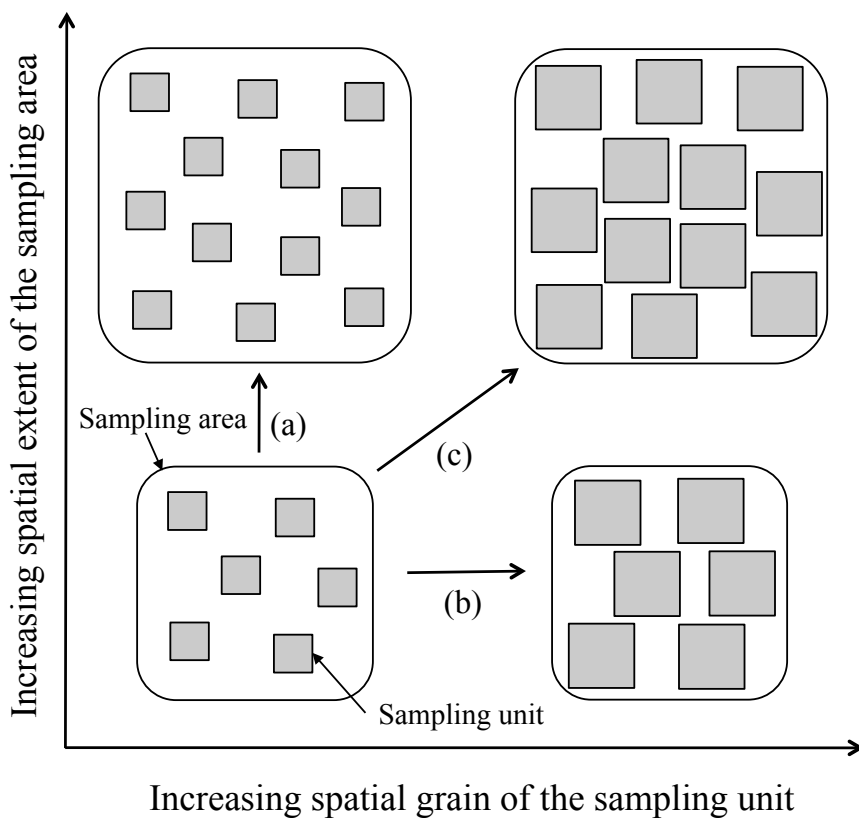
Figure 1. Interpretation of scale-dependence in ecological phenomena depends sensitively on how the spatial grain of sampling units and the spatial extent of the sampling area are defined and scaled (after Anderson *et al*. 2011). The ways in which spatial grain and extent may scale include (a) fixing 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.

566
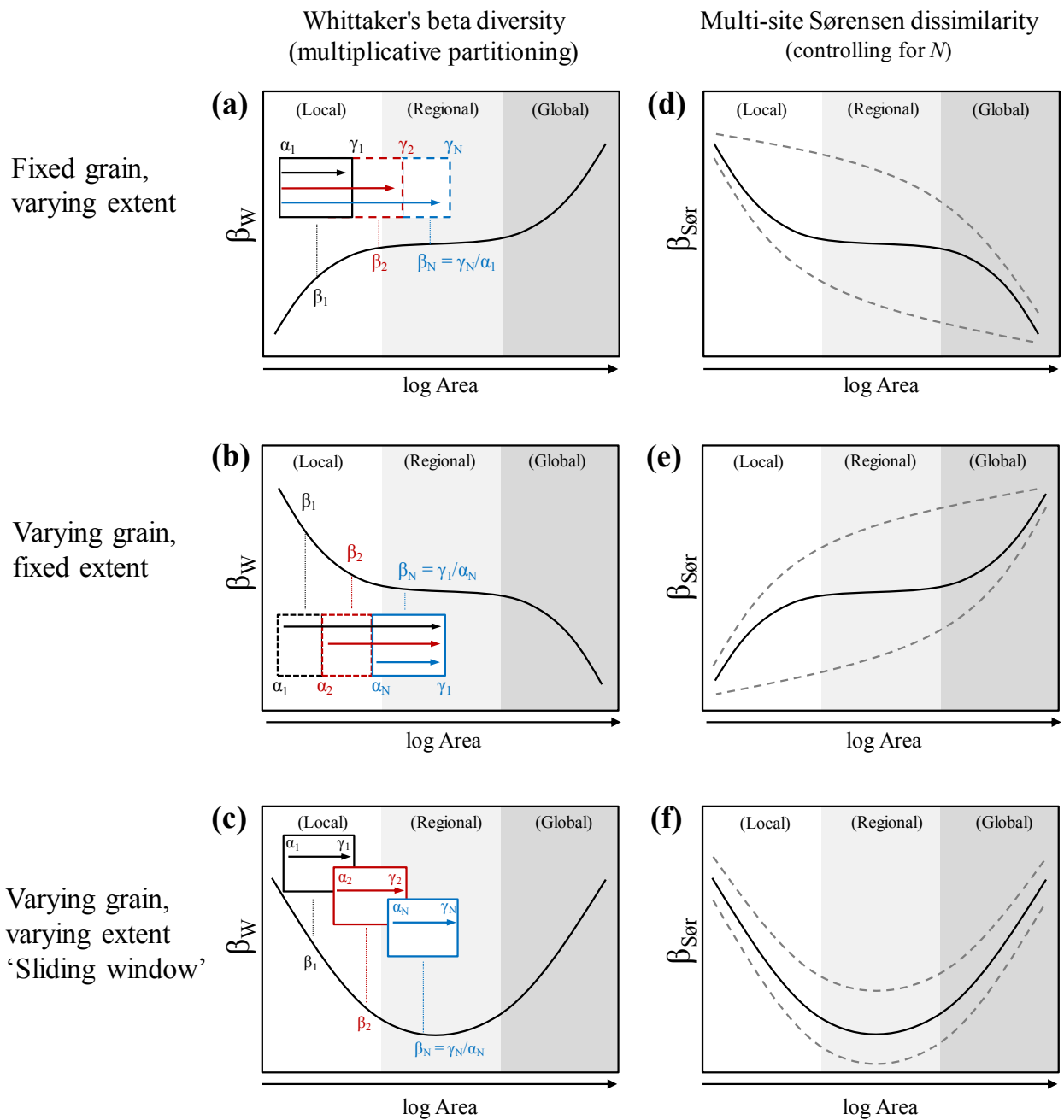
Figure 2. Conceptual approaches to the spatial scaling of β-diversity can be derived from the interaction between sampling grain and study extent, which define the 'spatial window' of observation. The spatial grain of sampling units will define the scale of α-diversity, and the spatial extent of a study will define the scale of γ-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 β-diversity will: (a) increase monotonically if the spatial scale of α-diversity is fixed but the scale of γ-diversity is allowed to vary; (b) decrease monotonically if

25

575   the spatial scale of γ-diversity is fixed, but the scale of α-diversity is allowed to vary; and (c) exhibit

576   a concave parabolic curve if the spatial scales of both α and γ vary together (a 'sliding window').

577   Aggregate measures of beta can be confounded by the number of sampling sites (N) compared,

578   which intrinsically decline as spatial grain increases, but increase as spatial extent increases. A

579   normalised measure of beta that controls for N, such as one minus the multiple-site Sørensen

580   similarity index (β_{Sor}), will produce curves in the opposite direction to Whittaker's beta diversity

581   when either (d) grain, or (e) extent is fixed, representing the change in average dissimilarity among

582   sampling units at that scale. The logistic scaling relationship illustrated here is based on generalised

583   assumptions about the underlying mechanisms detailed in Table 1. These assumptions, however,

584   may not hold in all cases, and we suggest that actual empirical scaling curves of beta diversity are

585   likely to vary from simple linear to complex logistic relationships (dashed lines in (d), (e), and (f)),

586   depending on the range of spatial scales considered, the structure of the sampling design, the

587   measure of beta diversity, and the taxon or biogeographic areas being examined. Importantly, both

588   measures of beta diversity will produce the same concave curve when grain and extent are allowed

589   to co-vary using our 'sliding window' perspective (c) and (f).

590
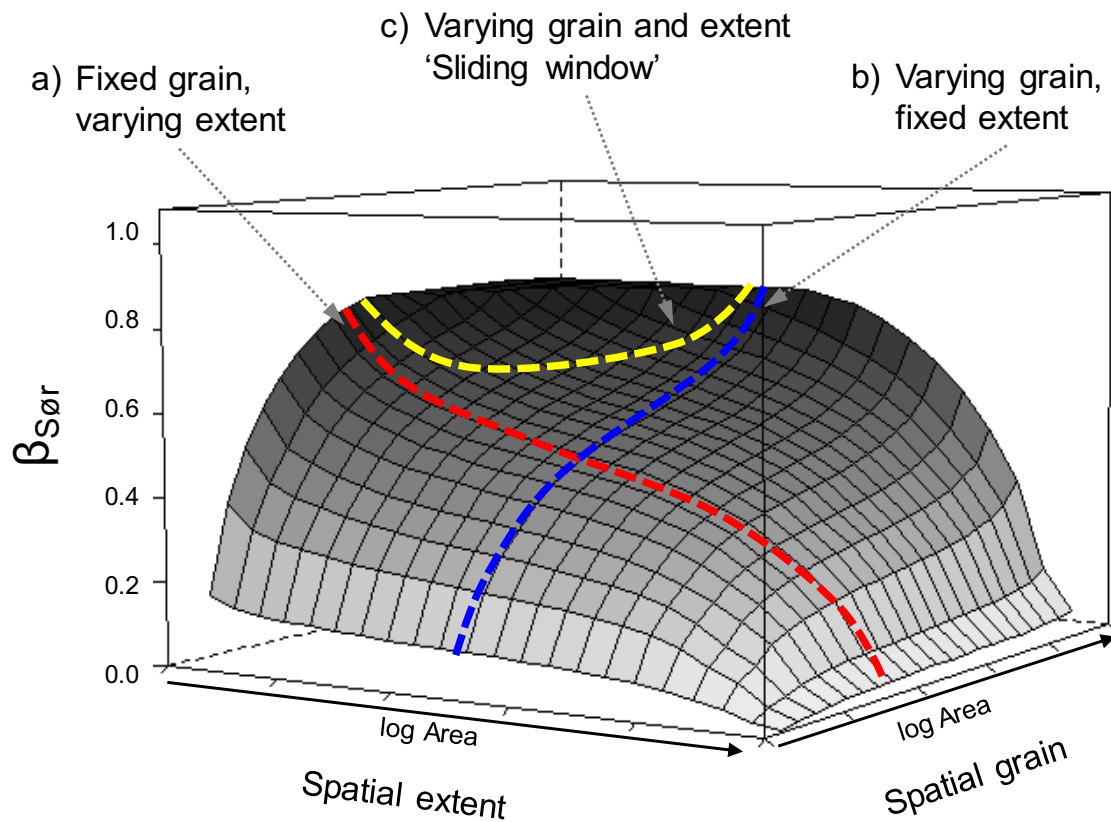
Figure 3. A general conceptual model for the spatial scaling of beta diversity. The three-dimensional surface shows schematically how varying spatial scales of sampling grain and study extent might influence beta diversity. Here, 'beta diversity' is depicted on the vertical axis as one minus the multiple-site 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.