



Peak beta diversity occurs at regional spatial grains

Leo Ohyama¹, Juan D. Bogota-Gregory², David G. Jenkins³

¹ University of Florida, Biodiversity Institute, Gainesville, FL, 32603, USA

² Instituto Amazónico de Investigaciones Científicas SINCHI, Leticia, Amazonas, Colombia

³ University of Central Florida, Department of Biology, Orlando, FL, 32816, USA

Corresponding author: David G. Jenkins (david.jenkins@ucf.edu)

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Abstract

Beta diversity (β) quantifies the dissimilarity between communities and is thus fundamental to biogeography and spatial ecology. However, multiple and conflicting hypotheses exist to explain how β varies with spatial scale (here grain within a constant extent). Some resolution on spatial scaling of β may help clarify long-standing debate about: (a) β itself and (b) the ecological community concept, because the clearest spatial size of an ecological community corresponds to the scale with maximal β . Here we test five alternative hypotheses for β spatial scaling by calculating β for four very different taxa (ants, birds, diatoms, and trees) at spatial grains ranging from one to one million km² in a constant spatial extent (contiguous USA). We also test repeatability for: (a) summer and winter bird β in six consecutive years; (b) trees through time (4 years, spaced 5 years apart). Specifically, we organize point data into hexagonal polygons, and then calculate mean pairwise β between each hexagon and its neighbors. We also calculate the deviation of β from two null models (assuming either spatial heterogeneity or homogeneity). For multiple reasons, β deviation based on spatial heterogeneity was preferable to that based on spatial homogeneity. For all taxa, β peaks at regional scales: trees ~300 km²; winter birds ~500 km²; summer birds ~2000 km²; ants ~2000 km²; diatoms ~11,000 km². Also, spatial scaling is consistent inter-annually (birds, trees) and sensitive to seasonality (birds). Results broadly support the regional community concept and, based on the variety of taxa evaluated here, similar patterns are likely across the tree of life. Local ecological and evolutionary forces scale up to form regional community patterns and results here support efforts to coordinate local conservation efforts in regions (e.g., corridors and networks) to best conserve biodiversity.

Highlights

- Beta diversity peaked at substantial spatial scales for all taxa evaluated here (ants, birds, diatoms, trees), suggesting a general pattern.
- The regional community concept advanced by Robert Ricklefs is supported empirically, in preference to four other hypotheses also tested.
- Beta diversity calculations used a relatively new deviation from a spatially heterogeneous null, which modestly adjusted observed beta diversity.
- Results support use of this newer beta deviation rather than the older beta deviation based on spatial homogeneity.
- Given that ecological communities appear regional in scale, local biodiversity conservation work can best ensure success if it is regionally coordinated.

Keywords

ants, beta deviation, beta diversity, birds, diatoms, ecological community concept, spatial grain, spatial scale, trees

Introduction

Ecological communities are often defined as “multiple species living in a specified place and time” (e.g., Vellend 2010) and are an important focal point in ecology. This definition is purposefully flexible in its spatial scale (i.e., grain and extent; Wiens 1989) when referring to different study systems and taxa. However, it leaves hanging a question at the heart of critiques for ecology (McIntosh 1986; Wilson 1991; Lawton 1999; Ricklefs 2008; Roughgarden 2009; Vellend 2010): Are ecological communities

natural entities (i.e., they exist as particular and discrete units) or mere abstract concepts of convenience?

The absence of a clear answer to the question above has been an obstacle for a century's studies of biodiversity (McIntosh 1986) and continues to cause difficulty in biogeographical and ecological studies. Research on natural biodiversity has navigated around this obstacle by one of four paths. A common approach is to use an operational community definition (e.g., the first sentence above) to bear "as little conceptual baggage as possible, so that we can put the debate about their existence behind us" (Palmer and White 1994). Some disagree (e.g., Wilson 1994; Jax et al. 1998), leading to reliance instead on external proxies (i.e., not based on community patterns) such as geomorphology or habitat (e.g., Cadenasso et al. 2003; Fagan et al. 2003; Yarrow and Marin 2007). A third path is to focus instead on levels of organization that lie below (i.e., individual organisms or populations; Clark et al. 2011) or above (i.e., metacommunities; Leibold et al. 2004) the community level. Unfortunately, the fundamental problem remains for metacommunity ecology, which relies on local communities as basal units of study. Finally, Lawton (1999) and Ricklefs (2008) viewed the problem as one of scale, and Ricklefs (2008) argued that regional scales should be preferred to local scales in order to better address the full suite of selective conditions driving diversity. Here we work with spatial scale by varying resolution (i.e., grain) but holding spatial extent constant (Wiens 1989).

The lingering question and its decades of debate (summarized above) are relevant to effective conservation biogeography. Whereas conservation biology has steered toward single species (Simberloff 1988), conservation biogeography explicitly addresses multispecies biodiversity patterns (Whittaker et al. 2005; Richardson and Whittaker 2010), where clear patterns are required to best understand and address anthropogenic impacts. For example, spatial strategies such as coordinated corridors and networks among conserved sites (e.g., Rouget et al. 2006) may be most effective if targeted to scales best representing biodiversity patterns. If those scales of community biodiversity can be approximated well, then both lingering uncertainty on the ecological community concept, and the building blocks of conservation biogeography may be better resolved.

Here we assess the empirical spatial scale of communities by evaluating beta diversity (β), which represents the difference between two sets of species (Whittaker 1972; Tuomisto 2010; Anderson et al. 2011). We reasoned simply that maximal β indicates the clearest possible separation between neighboring communities, and so the corresponding spatial grain of this maximal β represents the optimal spatial scale of ecological communities. Our approach adopts long-standing logic from research on optimized spatial resolution in remote sensing (Woodcock and Strahler 1987), where an optimal grain size in a satellite image is needed to discern empirical objects without errors of omission expected at finer spatial grains and errors of commission expected at coarser spatial grains (Ming et al. 2011; Mutowo et al. 2023). The empirical "object" here

is β among neighboring hexagonal grids (Fig. 1a), where fine spatial grains may sample only common species but coarse spatial grains may be overly inclusive and essentially blur existing pattern. The spatial grain with maximal β is then the optimized balance between errors of omission and commission and indicates the empirical size of a community, given that scale finds the clearest differences between adjacent communities.

Maximal β was free to occur at any spatial grain within the million-fold range evaluated here. Diversity patterns of the focal organisms make no assumptions based on external landscape or habitat features because those are not used in analyses. Likewise, diversity patterns do not require information or make assumptions based on population or metacommunity biology (e.g., dispersal distances, etc.). Additionally, our approach obtains a quantitative gradient showing maximal β and its associated variance across spatial grains; as such, it does not presume *a priori* thresholds or categories. To detect such pattern is a precursor for potential subsequent research to understand mechanisms underpinning the pattern; our research simply seeks to identify spatial grains at which that research may best reflect community patterns. We work with data for four very different taxa (ants, birds, diatoms, and trees) that help to consider potential generality of pattern but also require we treat the community concept here as assemblages (Fauth et al. 1996; Stroud et al. 2015).

We tread carefully with both β and spatial scale, which are entangled throughout relevant literature and require brief explanation here. Enough confusion has accrued about β for it to be described as "a concept gone awry" (Tuomisto 2010) with a "confusing array of concepts, measures and methods" (Anderson et al. 2011). For clarity, the general beta diversity concept is denoted here by β , but specific versions have subscripts. Here we use a β based on a multiplicative relationship (i.e., $\beta = \gamma/a$), where γ is overall diversity and a is local diversity (Tuomisto 2010; Xing and He 2021). An even more important decision for our purposes here is to use a deviation of β from randomized expectations (e.g., β_{DEV}). This matters because β is a function of both γ and a . Thus, β in neighborhoods of sites with different γ and/or a will inherently differ but can be adjusted to evaluate spatial patterns more fairly by calculating the difference from randomizations conducted with the same data. Initially, β_{DEV} was calculated using a spatially-homogeneous null (Kraft et al. 2011), but a recent version based on spatial heterogeneity (called β_{NBD} for its underlying negative binomial distribution) can represent clustered patterns more accurately across spatially-varying regions (Xing and He 2021). Here we use β_{NBD} as our main measure of β but also compare results to β_{DEV} and observed β (β_{OBS}), where more details on the three β s are below in Methods and evidence of this secondary consideration is presented in Suppl. material 1.

Spatial scale is important to ecology because both patterns (e.g., β) and processes have inherent scales (Wiens 1989; Barton et al. 2013; Zhang et al. 2015); to discern well the process-pattern linkage requires matching scales.

Here we hold spatial extent constant as the contiguous USA ($8.08 \times 10^6 \text{ km}^2$) to evaluate the relationship between β and spatial grain (i.e., resolution) from 1.0 km^2 to 1 million km^2 . At each spatial grain, we compare a central hexagonal grid to each of its immediate neighbors (Fig. 1a) to obtain a mean pairwise β for each grid. Thus, the focal scale of analysis (Whittaker et al. 2001) for β is the neighborhood, where neighborhoods are constrained (i.e., $N < 6$ adjacent grids with spatial size = central grid) for all β estimates at all spatial grain sizes, and pairwise comparisons of grid cells (i.e., β) avoids errors inherent in other methods (Marion et al. 2017).

Based on prior research, β is expected to depend on spatial grain in at least five different ways (Fig. 1b), where that variety appears related (in part) to the variety of β measures and spatial scales that have been studied. If maximal β occurs at small spatial grains (Fig. 1b1), then locally-scaled communities would be supported (Keil et al. 2012; Barton et al. 2013). Alternatively, β may progressively increase with spatial grain, reflecting sample size effects (Fig. 1b2; Zhang et al. 2015; Keil and Chase 2019; Xing and He 2021). Both trends may occur but represent studies conducted at different spatial scales, so β may first decrease and then increase to follow a V- or U-shaped curve across a wider range of spatial grains (Fig. 1b3). Alternatively, the regional community concept (Ricklefs 2008) would be supported if β exhibited hump-shaped peaks at an intermediate spatial grain (Fig. 1b4), which would also be consistent with patterns of an optimized spatial grain (expressed as local variance) in remote sensing (Woodcock and Strahler 1987; Ming et al. 2011; Mutowo et al. 2023). In that research, optimal spatial grain is often at intermediate sizes, though outcomes vary, depending on the image. Finally, it is possible that β exhibits no clear trend with spatial grain (Fig. 1b5; Lira-Noriega et al. 2007).

Xing and He (2021) cautioned about potential effects of spatial scale on β and deviations of β from null models (β_{DEV} or β_{NBD}), and wrote “the same grain size and similar spatial extent are required when β or β -deviation is compared among different regions.” We paid heed, and vary only one potential effect (i.e., spatial scale) while holding the other two effects (extent and region of interest) constant while evaluating responding β and β deviations.

If spatial scale is composed of two axes (grain and extent), a third and related axis is represented by study scale, often measured as sample size (e.g., Jenkins 2011; Xing and He 2021). Study scale can affect observed β if larger

areas include more samples that enable the detection of more species, as expressed in rarefaction of species-sample curves (Chao et al. 2014). We addressed study scale effects across spatial grains using both a *a priori* and a *posteriori* approaches.

Beyond β scaling shape (Fig. 1b), differences in the details among taxa could inform long-standing questions of dispersal scaling of diversity among microbial and macroscopic organisms (Fontaneto 2011). Assuming similar general β spatial scaling shapes across taxa, we expected diatoms to exhibit smaller spatial grains for peak β than other taxa because: diatoms exist within hard ecotones (i.e., lake shores here); are sensitive to local water quality (Reid et al. 1995); and most species inhabit one or few lakes (USEPA 2009). In comparison, species of trees, ants and birds inhabit intergrading habitats, have aerial life stages, and/or inhabit substantial ranges. In combination with the general scaling of dispersal distances for actively dispersing organisms (Jenkins et al. 2007), we expected spatial scales of peak β_{NBD} would rank as diatoms < ants < trees < birds.

Methods

Data acquisition and management

We obtained data for the contiguous USA for ants (Guénard et al. 2017), birds (Sullivan et al. 2009), diatoms (USEPA 2009), and trees (USDA Forest Service 2019; Table 1). Ant data represented cumulative records synthesized from literature records and existing databases. Before analysis, we removed any ant observations marked as dubious or needing confirmation. The eBird system (Sullivan et al. 2009) amasses standardized community science data, including the number of birds per species, number of observers and time spent. Bird data analyzed here represented cleaned reports from January and July during 2010–2015. We expressed bird abundances per unit effort (i.e., per person-hours) to standardize among reports. We used January to represent winter conditions and July to represent summer conditions. Diatom data analyzed here were collected during one year from the top 5 cm of lake sediment and processed according to standardized protocols (USEPA 2009).

Data for trees (i.e., stems with diameter at breast height > 5 cm) were extracted from the US Forest Service’s Forest Inventory Analysis (FIA) data using the rFIA package in R

Table 1. Summaries of analyzed data sets.

	Ants	Birds	Diatoms	Trees
Number of species	699	1,560	1,957	403
Number of samples	24,893	810,921	1,070	39,396
Temporal range	2 centuries	2010–2015	2007	2002–2017*
Data type	presence	Mean count per person-hour	presence	presence
Temporal analyses?	No	Yes; seasonal	No	Yes; annual
Data Source	Guénard et al. (2017)	Sullivan et al. (2009)	USEPA (2009)	USDA (2019)

* 5-year increments.

(Stanke et al. 2020; R Core Team 2021). The years 2002, 2007, 2012, and 2017 were used for analyses here because they had similar numbers of samples and were evenly separated in time. More information on FIA’s standardized sampling protocols is available at <https://www.fia.fs.usda.gov/library>. Geographical locations of forest sample data in FIA are “fuzzed” by <1 mile (1.6 km) and 20% are “swapped” with another similar, nearby property to shield private lands in the publicly-available data (Burrill et al. 2021). Accordingly, we truncated the lower limit for overall mean β spatial scaling of trees to 10 km², or 10-fold greater than other data sets.

Data analyses

Each taxon was analyzed similarly using an iterative process summarized here, based on multiple R packages (R Core Team 2023). Georeferenced data were cleaned for uncertain species identities and intersected with hexagonal grids, where size of the cell was spatial grain. Where data represented counts (birds and trees), one datum per species per hexagon was obtained by averaging point data. Bird counts were standardized as mean count per person-hour, rounded up to the nearest whole number. Data for ants and diatoms were presence/absence; a species present somewhere in a hexagonal grid was listed as present.

Hexagonal grids and their 1st-degree adjoining neighbors comprised a neighborhood (Fig. 1a). All β calculations were conducted between a central grid and each of its neighbors, where a lower limit for calculations of means was that a neighborhood included at least three grids and 3 species. Finest spatial grains were most likely affected by this threshold because small grids could be empty of species. This process was repeated at spatial grains (i.e., hexagonal grid areas) from 1 km² to 1 million km² (i.e., 1, 5, 10, 50, ... etc.; 13 spatial grains in total). The 1 and 5 km² grains were omitted in analyses of trees for reasons explained above. Mean pairwise β for each hexagon enabled fair comparisons among hexagons within and among spatial grains.

By working with hexagonal grid cells and their neighbors, study size was standardized into the number of grids. We compared each grid cell to each of its adjoining neighbors, where hexagonal grids are constrained to have < 6 neighbors (thus controlling grid sample size across spatial grains). A tradeoff may still linger, where smaller grid cells contain too few samples for reliable diversity estimation (i.e., errors of omission) but very large grid cells are so inclusive as to blur actual patterns (i.e., errors of commission; Boschetti et al. 2004). Thus, we also evaluated *a posteriori* any lingering effects of sample size *per se* (i.e., the number of data points within a hexagonal grid) on results across spatial grains. We also evaluated effects of neighborhood size (M) and species richness (S) on β measures to show that the use of β_{NBD} is supported (Suppl. material 1), whereas β_{DEV} is problematic, consistent with results of Xing and He (2021).

Data for birds and trees enabled comparisons within each data set (Table 1); we analyzed bird data for winter and summer in each of six consecutive years to evaluate sensitivity of this approach to seasonal changes and inter-annual repeatability of those patterns. We hypothesized that seasonal migrations would concentrate winter birds in the southern USA compared to summer to cause reduced: (a) spatial scale of bird communities (i.e., the grain at which peak β_{NBD} occurs); and (b) magnitude of peak β_{NBD} . We also expected annual re-assembly cycles in bird communities would result in repeatable spatial scaling and patterns during the 6-year span. Similarly, we hypothesized similar β spatial scaling of trees at four equally-separated years with similar sample numbers during a 15-year span despite varied sample locations each year.

We calculated three β versions using code from Xing and He (2021); a classic observed β and two ways to estimate deviation of β from null expectations (β_{DEV} and β_{NBD}). We emphasize β_{NBD} below, but to be complete also present in Suppl. material 1 the results for observed β and β_{DEV} . Observed β was calculated as:

$$\beta_{\text{OBS}} = 1 - \frac{\bar{\alpha}}{\gamma} \tag{Eqn. 1}$$

where α = mean number of species in a hexagon and γ = total number of species in the pair of hexagons being compared; Tuomisto 2010). Also, the spatially-homogeneous deviation (β_{DEV} ; Kraft et al. 2011) is calculated as:

$$\beta_{\text{DEV}} = \frac{\beta_{\text{OBS}} - \beta_{\text{NULL}}}{\sqrt{\text{var}_{\pi}(\beta_{\text{NULL}})}} \tag{Eqn. 2}$$

where β_{NULL} is:

$$\beta_{\text{NULL}} = \frac{\ln(1-p(1-\frac{1}{M}))}{\ln(1-p)} \approx \frac{\ln(\frac{M}{1+\lambda M})}{\ln(1/\lambda)} \tag{Eqn. 2a}$$

and var_{π} is the variance of β in the null model, M is the size of the metacommunity relative to the size of the local community (constrained here to <7), and $p = e^{-\lambda}$, related to a log-series species-abundance distribution and determined by N (total number of individuals) and S (total number of species; see Xing and He (2021) for details). Note that the approximation uses only M and λ , which is valid where M > 1 and $\lambda < 1$, as expected for real applications (Harte 2011; Xing and He 2021). The null model above (β_{NULL} ; Kraft et al. 2011) is based on a randomized spatial distribution of species while preserving overall species abundance distribution.

Xing and He (2021) explained three problems with β_{DEV} ; two are pragmatic and one is fundamental due to the meaning of β_{NULL} . Pragmatically, β_{DEV} is vulnerable to sampling effort and uses abundance data, where a method for presence/absence data is also needed. Fundamentally, β_{DEV} measures deviation from β_{NULL} , and thus estimates the effect of non-random spatial distribution of species on β . This meaning was known but ignored (Xing and He 2021) while β_{DEV} was instead interpreted as reflecting deviation “from a null model that corrects for γ dependence” (Kraft et al. 2011).

Spatial randomness (as in β_{NULL}) may apply in some cases, but spatial aggregation at all scales is well known (e.g., Fisher 1935) and often described as Tobler's First Law of Geography (Sui 2004). A null based on spatial aggregation should then be more useful to represent natural patterns than one based on spatial randomness. Accordingly, Xing and He (2021) derived a beta deviation based on negative binomial distributions (thus β_{NBD}) to represent spatial aggregation:

$$\beta_{NBD} = \frac{-1}{\ln(1-p)} \sum_{n=1}^{\infty} \frac{p^n}{n} \left(1 + \frac{n}{Mk}\right)^{-k} \approx \frac{\ln\left(\frac{M}{1+\lambda M}\right) + C(k, \lambda M)}{\ln(1/\lambda)} \quad \text{Eqn. 3a}$$

where n is species abundance and k represents aggregation, with smaller values indicating more aggregated distributions. As above, note that the approximation uses only M and λ , plus a term $C(k, \lambda M)$ which itself can be approximated as:

$$C(k, \lambda M) \approx \frac{\ln\left(\frac{1}{\lambda M} + 1\right)}{1 - (5.07 - 0.44 \ln(\lambda M))k} \quad \text{Eqn. 3b}$$

We used β_{NBD} to evaluate alternative hypotheses (Fig. 1b) in two ways. First, we used general additive models to fit $\beta_{NBD} \sim$ spatial grain curves to data, where each point represented a mean β_{NBD} (+ 95% confidence intervals) at a given spatial grain size. We also evaluated β_{NBD} distributions at each grain size to better understand variation around means (and thus the veracity of those means). Graphical results were generated using ggplot2 and ggridges in R (Wickham 2016; Wilke 2022). Secondly, we compared linear and quadratic models of $\beta \sim$ spatial grain, using Akaike Information Criteria weights (computed with bbmle in R; Bolker et al. 2022), corrected for sample size (i.e., $AIC_C w_j$), which represent the probability that a model is most efficient among those compared (Burnham and Anderson 2002). Model coefficient signs for the most plausible model then identified curve direction. Maps of mean pairwise β_{NBD} informed interpretations, and comparisons of β_{NBD} to β_{DEV} and β_{OBS} confirmed the results of Xing and He (2021), including the advantages of β_{NBD} relative to β_{DEV} .

We also evaluated potential sample size effects on β_{NBD} results, because β_{DEV} increases with greater sample size but such an effect was undescribed for β_{NBD} by Xing and He (2021). Because sample size can be measured in different ways, we examined sample size as: number of sample points in hexagons, number of hexagons contributing to a mean β_{NBD} at a spatial grain, neighborhood size (constrained for hexagons to <6), and species richness.

In summary, we controlled for scaling effects of spatial extent and sample size to evaluate potential $\beta \sim$ spatial grain relationships. We then evaluated mean pairwise β (in several forms) among spatial hexagons across a million-fold range of sizes for four very different taxa (ants, birds, diatoms, and trees). Because data sets differed substantially in their sources, subject taxa, and features (Table 1), we reasoned that similar β scaling shape (i.e., a general line shape in Fig. 1b) across datasets could indicate generality for varied taxa and data origins. However, we expected data sets to differ in details of β scaling (e.g., spatial grain matching a peak β).

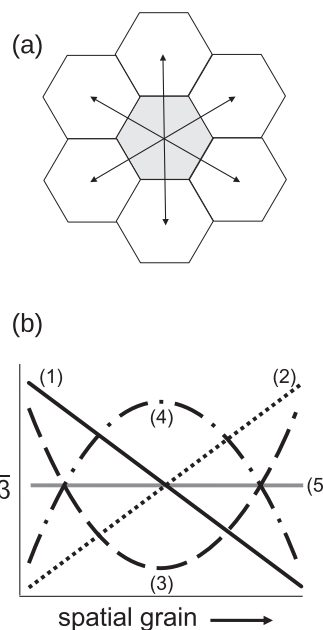


Figure 1. (a) Beta diversity (β) was calculated for each central hexagon as the mean of its pairwise β with its adjoining neighbor hexagons. (b) Hypothetical shapes of beta diversity spatial scaling. As spatial grain increases, beta diversity may (1) decrease because diversity patterns are caused by local processes (e.g., Barton et al. 2013; Keil et al. 2012); (2) increase because more samples at greater grain increase beta diversity (e.g., Zhang et al. 2015; Keil and Chase 2019; Xing and He 2021); (3) first decrease and then increase because both effects in (a) and (b) occur or have been studied at different scales; (4) peak at intermediate scales because diversity patterns are caused by regional processes (Ricklefs 2008); or (5) be uninformative (e.g., Lira-Noriega et al. 2007).

Results

Ants, birds, diatoms, and trees all demonstrated peak β_{NBD} at intermediate spatial grains that were roughly consistent in shape (Fig. 2), despite wide differences in natural history and data properties (Table 1). As may be expected for ants, birds, and diatoms from Fig. 2, hump-shaped quadratic curves (i.e., peak β_{NBD} at intermediate spatial grains) more efficiently represented data than linear models that would have supported some other scaling hypotheses depicted in Fig. 1 (all AIC_C weights > 0.95). Moreover, curve coefficients supported hump-shaped curves rather than V- or U-shaped curves. Trees exhibited a second but highly variable peak β_{NBD} at greatest spatial grains, which made null models more plausible than linear or quadratic models. The impact of grains of 500,000 and 1 million km² on that analysis was demonstrated by omitting them from analyses; then hump-shaped patterns were confirmed (AIC_C weights > 0.95). The broadly consistent result across very different taxa and data sets were consistent with the regional community concept. Moreover, interannual or interseason variation (where possible; birds, trees) indicated remarkable consistency.

Within that broad pattern, values of peak β_{NBD} (Fig. 2) differed substantially among taxa, and our hypothesis

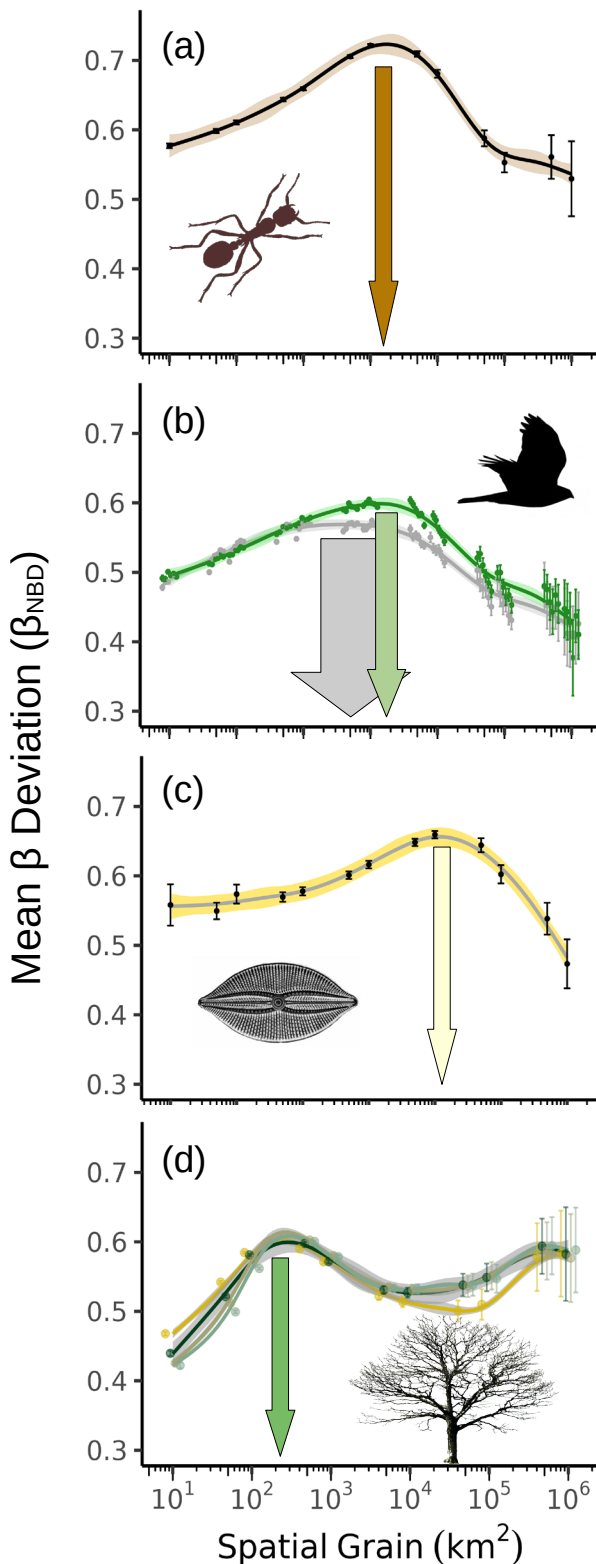


Figure 2. Spatial scaling of beta diversity, calculated as deviation from a null expectation ($\beta_{NBD} = 29$) and potentially ranging 0–1. β_{NBD} scaling of (a) ants; (b) birds (summer = green; winter = grey, 2010–2015); (c) diatoms; and (d) trees (2002, 2007, 2012, and 2017). Arrows indicate spatial grains corresponding to approximate peak β_{NBD} . Note log scale for spatial grain. Public domain organism images.

about the rankings of β_{NBD} was incorrect. Peak mean β_{NBD} for ants was about 1,500 km² (Fig. 2a). Peak mean β_{NBD} values for birds were about ~ 2,000 km² in summer but substantially reduced to roughly 500 km² in winter (green and gray vertical arrows in Fig. 2b, respectively). Peak mean β_{NBD} values were greatest for diatoms (~11,000 km²; Fig. 2c), but for trees peak mean β_{NBD} values were consistently at about 300 km² through 4 evaluated years spanning 2 decades (Fig. 2d). Mean β_{NBD} for trees increased again at greatest spatial grains, but with wide confidence intervals (Fig. 2d), for reasons we explain below, and which led us to disregard the second peak. Tree mean β_{NBD} values at about 300 km² had very little within- or among-annual variation (95% confidence intervals are smaller than symbols in Fig. 2d). Thus, we ranked peak mean β_{NBD} among taxa as [trees < winter birds < ants ≈ summer birds < diatoms], rather different from our naive hypothesis (diatoms < ants < trees < birds).

We also evaluated variation of β_{NBD} as a function of spatial grain, where each central hexagon’s mean β_{NBD} contributed to a plotted distribution (note the “flipped” axes between Figs 2, 3). Essentially, wider confidence intervals around peak mean β_{NBD} (Fig. 2) were related to the number of hexagons contributing to a mean (e.g., only 14 at 1 million km² grain) and variation in mean β_{NBD} values (Fig. 3). Ants had substantial variation in β_{NBD} at any one spatial grain (Fig. 3a), where multimodal distributions of β_{NBD} were apparent at both smallest and greatest grains but unimodal and narrower distributions at peak β_{NBD} were most appropriate for a mean (Fig. 3a). Birds had remarkably narrow β_{NBD} distributions, so mean values in Fig. 2 represented patterns quite well regardless of season at spatial grains < 500,000 km² (Fig. 3b, c). Like ants, distributions for diatoms were multimodal at smallest and greatest grains but appropriate to a mean value at intermediate grains where peak values occurred (Fig. 3d). Distributions for trees supported the use of mean peak β_{NBD} values at smaller grains, but multimodal and wide variation at greater grains reduced validity of a mean to represent patterns (Fig. 3e). In all cases, spatial grains with peak β_{NBD} obtained data distributions most appropriately described by a mean and confidence intervals, whereas other spatial grains represented more problematic distributions. Thus, distributions of mean β_{NBD} (Fig. 3) validated inferences about peak mean β_{NBD} values at intermediate spatial grains across taxa analyzed here.

Deviation of β from a null model based on spatial homogeneity (β_{DEV}) increased with sample size as expected, but β_{NBD} did not. Instead, β_{NBD} consistently peaked at intermediate grain sizes that corresponded to intermediate numbers of samples, hexagons, species, and neighboring hexagonal grid cells. Based on results above (Figs 2, 3) and additional results summarized here (details are in Suppl. material 1), mean pairwise β_{NBD} was not a simple progressive function of sample size, which could confuse results; because bigger hexagons can include more observation locations. This detail is secondary to our main question here but is important to an alternative hypothesis that β

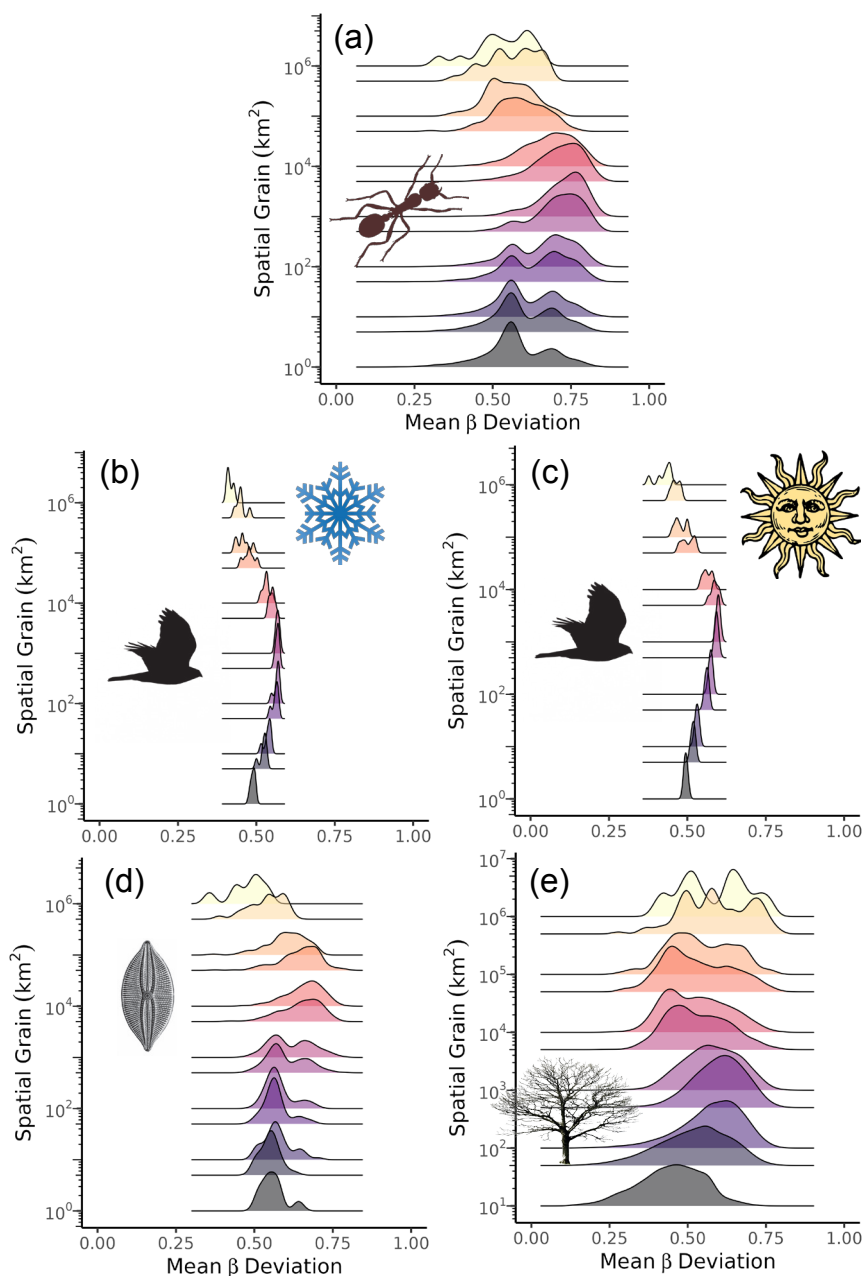


Figure 3. Data distributions for beta diversity, calculated as deviation from a null expectation (β_{NBD} ; Xing and He 2021) and potentially ranging 0–1. Normal data are best represented by means, and narrow variance generates narrow confidence intervals (see Fig. 2). (a) Ant β_{NBD} was most variable and multimodal at small and large spatial grains. Bird β_{NBD} in both (b) winter and (c) summer was relatively narrow overall but especially suited to means at peak β_{NBD} . (c) Similar to ants, diatoms were best represented by means at peak values. (d) Trees data were multimodal at greatest spatial grains. Note log scale for spatial grain.

simply scales with sample size (e.g., Fig. 1b) and because β has been historically calculated in multiple ways. Moreover, peak β_{NBD} occurred at different spatial scales among taxa despite having data assigned to identical base hexagonal maps at each grain size, indicating that the methods adopted did not cause roughly-similar patterns to emerge. In all, multiple lines of evidence demonstrated that sample size effects were not important contributors to patterns in spatial scaling of mean pairwise β_{NBD} . Also, β_{NBD} repeatedly represented a modest adjustment to β_{OBS} whereas β_{DEV} represented substantial changes relative to β_{OBS} .

Discussion

Results here help address decades of confusion about beta diversity (β) and spatial scaling, and the conceptual reality and practical value of ecological communities (Whittaker 1972; McIntosh 1986; Wilson 1991; Lawton 1999; Ricklefs 2008; Roughgarden 2009; Tuomisto 2010; Vellend 2010; Anderson et al. 2011; Chave 2013). As such, it helps better resolve units of study and action for conservation biogeography (Whittaker et al. 2005). Work here was based on the premise that an entity is best measured by its

own properties, and thus β (i.e., differences between communities) patterns can indicate a spatial scale that most clearly differentiates between neighboring communities. We obtained empirical gradients of β across spatial grains, which were free to form inherent shapes and where peak values represented spatial scales of the maximal differences between adjoining communities. Below we elaborate on lessons learned regarding β , ecological communities, interdisciplinary methods, and implications for conservation.

While β is a fundamental measure of ecological diversity patterns (Whittaker 1972), it has a long history of disputes spanning its concepts and metrics that largely coincided with debate on the veracity of ecological communities. Work to organize research on β (e.g., Tuomisto 2010; Anderson et al. 2011) made it more clearly understood, including the use of deviations from null expectations (β_{DEV} ; Kraft et al. 2011) that led to the recent update based on spatial heterogeneity (β_{NBD} ; Xing and He 2021) used here. We showed that β_{NBD} moderately adjusted observed β values (β_{OBS}) and did not introduce sample size effects, unlike β_{DEV} which greatly altered β_{OBS} and was subject to sample size effects. Thus, results here among very different taxa and data sources support the value of β_{NBD} (Xing and He 2021) for future research on β diversity.

Very different taxa (and data origins) obtained a remarkably consistent general shape for β spatial scaling here (and yes, differences existed in the details). If this general pattern holds among other taxa across the tree of life and different data sources, some generality is enticingly possible for the spatial scaling of biodiversity patterns and the regional community concept. Moreover, spatial scaling of β_{NBD} for birds and trees is inter-annually repeatable and (for birds) sensitive to seasonal conditions, suggesting stability of β_{NBD} spatial scaling. What processes might cause such general patterns? Much of our collective understanding of ecological processes is necessarily obtained at local scales much finer than those used here, related to historical and logistical limits on data collection.

We stress that results here do not disavow local-scale research, which is vital to understand mechanisms of biotic and abiotic interactions and provided data amassed here and then integrated into a variety of spatial units. However, results here support efforts to better understand how myriad local processes (i.e., abiotic and biotic interactions affecting individuals or demes) cascade up to cause regional patterns, and to compare those local processes to regional processes (Ricklefs and Schluter 1993; Ricklefs 2008; D'Amen et al. 2017). Also, we may infer that local and/or regional processes acting on individuals, demes, or a species must be general enough to translate to regional β diversity patterns detected here, consistent with Ricklefs' (2008) regional community concept.

Results for birds and trees indicate spatial scaling of β_{NBD} is inter-annually repeatable and (for birds) sensitive to seasonal conditions. Given that birds and trees differ so greatly in life histories and mobility, this commonality suggests community assembly processes are a strong and common basis for β_{NBD} spatial scaling. Future work on the spatial scales of

those processes, including effects of habitat heterogeneity, may help explain the regional scales observed here. Interestingly, ants and summer birds had roughly similar regional community scales, perhaps related to similar scales of factors that control distributions of birds and founding ant queens that establish colonies (Helms et al. 2016). Finally, differences in bird β_{NBD} scaling between summer and winter indicate that the approach here is sensitive to temporal conditions across substantial extent (contiguous US). Given this pattern, changes in β_{NBD} scaling over longer terms may represent effects of changing climate and/or land cover.

Results here also inform the dispersal scaling of communities, where potential long-range dispersal of microscopic organisms has long been debated as causing greater global taxonomic similarity than observed for macroscopic organisms (Fontaneto 2011). At first glance, spatial scaling of β_{NBD} for diatoms appeared to support long-range dispersal scaling of microbial diversity. However, community size of lake diatoms roughly matched the average sampled lake density (1071 sampled lakes / 8.08×10^6 km² in the contiguous US = 1 lake / 1.3×10^4 km²), and the majority (52%) of species were recorded in <3 lakes. Thus, diatom results here are consistent with a diatom community being bounded by one lake shore, on average. Spatial scaling of diatom β_{NBD} may actually represent the average dispersion of sampled discrete diatom habitats, in contrast to intergrading terrestrial habitats represented here for ants, birds, and trees. If so, other microbial communities (e.g., soils) sampled at greater spatial density may be evaluated with the approach here to further evaluate dispersal scaling of microbial community structure.

The community concept has been debated almost since its origin (McIntosh 1986; Wilson 1991; Lawton 1999; Ricklefs 2008; Roughgarden 2009). Ecology and biogeography have nonetheless progressed, often by ignoring this problem. At the same time, scale became widely recognized as fundamental to understand natural processes and patterns (Chave 2013), and β emerged (with its many versions; Tuomisto 2010, Anderson et al. 2011) as an important measure in ecology and biogeography. In that context, ecology has (in part) expanded toward biogeographical spatial scales (Lawton 1999; Leibold et al. 2004; Roughgarden 2009; Jenkins and Ricklefs 2011). Results here support this fusion by showing empirical differences between adjacent communities are most apparent at regional scales (i.e., hundreds to tens of thousands of km²), consistent with the regional community concept (Ricklefs 2008).

In that theme, a regional community has been interpreted as the scope of an entire metacommunity (Jenkins and Ricklefs 2011). Results here support that view and point to a way to identify the potential size of a regional community / metacommunity / regional source pool, whether for broad taxa (as done here) or more specific subsets (e.g., based on habitat use or traits). However, the same old problem (see Introduction) remains for the subsequent definition of local communities within a metacommunity. Relatively low β_{NBD} at fine scales here supports the argument of Ricklefs (2008) that local communities are one end of spatiotemporal

continua, rather than empirically distinct entities. Much of metacommunity ecology may be wise to treat local communities as sample points rather than empirically bounded, discrete units. This view steers metacommunity ecology away from the frail local community concept and toward a species-centric approach (Ricklefs 2008; Jenkins 2011) that is conceptually consistent with hierarchy theory (Allen and Starr 1982). Alternatively, if one regards results here to indicate a single community is $\sim 10^3$ km², then a metacommunity is vast – perhaps too vast for the metacommunity concept to be useful. We prefer the former view.

Long-standing work in remote sensing to optimize spatial resolution of images (e.g., Woodcock and Strahler 1987; Ming et al. 2011; Mutowo et al. 2023) provides lessons for how biogeography may improve understanding of spatiotemporal patterns. Modern biogeography relies heavily on spatially-distributed data in multiple ways, including rasterized representations like those used here. Both old (e.g., Woodcock and Strahler 1987) and new (e.g., Wylie et al. 2019) practical lessons from remote sensing and GIS can be fruitfully applied in biogeography. This may seem obvious, but the fact that optimized spatial resolution does not seem to have been applied to β justifies making the point here. Other biogeographical patterns may also exhibit similar peaked spatial scaling that may help reveal maximal signal amidst the noise to better represent natural patterns than making maps with tidy space filling or visual appeal. If so, various ecological and biogeographical concepts tested so far at widely varying spatial grains (and then debated) may gain better resolution.

Finally, our results bear fundamental implications for conservation biogeography in the Anthropocene because they indicate that regional scales are appropriate to conserve biodiversity (Whittaker et al. 2005). Thus, our results add importance to work toward corridors and networks among conserved sites (e.g., Rouget et al. 2006), and may help researchers reconsider the appropriate spatial grains to use when studying diversity responses to land use and climate change. For example, a study to evaluate diversity responses to changing land use and climate may obtain maximal resolution by using rasterized units of study that match peak β .

Data Accessibility Statement

All data analyzed here were obtained from publicly-accessible sources, cited in References. Code central to calculate β in all forms here is provided by Xing and He (2021).

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Supplementary materials

Supplementary material 1

Supplementary figs S1–S6 (.pdf)

Link: <https://doi.org/10.21425/fob.17.132675.suppl1>