

Spatial scale modulates the inference of metacommunity assembly processes

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Abstract. The abundance and distribution of species across the landscape depend on the interaction between local, spatial, and stochastic processes. However, empirical syntheses relating these processes to spatiotemporal patterns of structure in metacommunities remain elusive. One important reason for this lack of synthesis is that the relative importance of the core assembly processes (dispersal, selection, and drift) critically depends on the spatial grain and extent over which communities are studied. To illustrate this, we simulated different aspects of community assembly on heterogeneous landscapes, including the strength of response to environmental heterogeneity (inherent to niche theory) vs. dispersal and stochastic drift (inherent to neutral theory). We show that increasing spatial extent leads to increasing importance of niche selection, whereas increasing spatial grain leads to decreasing importance of niche selection. The strength of these scaling effects depended on environment configuration, dispersal capacity, and niche breadth. By mapping the variation observed from the scaling effects in simulations, we could recreate the entire range of variation observed within and among empirical studies. This means that variation in the relative importance of assembly processes among empirical studies is largely scale dependent and cannot be directly compared. The scaling coefficient of the relative contribution of assembly processes, however, can be interpreted as a scale-integrative estimate to compare assembly processes across different regions and ecosystems. This emphasizes the necessity to consider spatial scaling as an explicit component of studies intended to infer the importance of community assembly processes.

Key words: community assembly; dispersal; ecological drift; metacommunity; neutral theory; niche selection; sampling grain; spatial extent; spatial scale.

INTRODUCTION

The abundance and distribution of species across the landscape depend on the interaction between multiple processes, including habitat heterogeneity, dispersal and ecological drift (e.g., Leibold et al. 2004, Gravel et al. 2006, Vellend 2010, 2016, Leibold and Chase 2017). Despite the relatively straightforward way to delineate these basic assembly processes conceptually, empirical evidence describing their relative importance has been more challenging. For example, early tests of the importance of dispersal and drift inherent to the neutral theory, as opposed to niche theory, focused on one-dimensional patterns such

as the shape of the species abundance distribution (e.g., McGill 2003 vs. Volkov et al. 2003) or distance-decay relationship (e.g., Condit et al. 2002 vs. Tuomisto et al. 2003). However, these pattern analyses alone are unlikely to be able to distinguish the relative importance of different processes (e.g., Chave et al. 2002, Chisholm and Pacala 2010, Münkemüller et al. 2012, May et al. 2015). As a result, considerable emphasis has been placed on using multivariate analytical tools as a means to disentangle the relative importance of different community assembly processes (e.g., Peres-Neto et al. 2006, Shipley et al. 2012, Monteiro et al. 2017, Ovaskainen et al. 2017).

One of the most popular approaches for exploring the relative importance of different metacommunity assembly processes has been the use of multivariate methods (e.g., Borcard et al. 1992, Peres-Neto et al. 2006) to partition the effects of environmental factors (typically associated with niche-related processes) and spatial factors (typically

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associated with neutral-related processes) in determining community structure (e.g., Gilbert and Lechowicz 2004, Cottenie 2005, Legendre et al. 2009, Soininen 2014, 2016). While variation partitioning to infer environmental (and spatial) correlates of community structure remains an important tool, it has a number of limitations. Some of these are statistical (e.g., Gilbert and Bennett 2010, Smith and Lundholm 2010), while others are more theoretical, for example, when certain niche-based mechanisms (e.g., frequency dependence or priority effects) nevertheless result in weak correlations of community structure with environment (e.g., Leibold and Chase 2017).

Despite recent improvements in the analytical methods used to infer environmental vs. spatial (and interspecific) associations of species in metacommunities (Layeghifard et al. 2015, Monteiro et al. 2017, Ovaskainen et al. 2017), a largely overlooked but critical feature of any metacommunity is the spatial scale at which it is observed (but see Legendre et al. 2009, Chase 2014, Leibold and Chase 2017). While the fundamental importance of spatial scale in influencing process and pattern in community ecology has been recognized for decades (e.g., Shmida and Wilson 1985, Wiens 1989, Levin 1992, O'Neill et al. 1996), these scaling relationships are rarely considered in theoretical or empirical investigations of metacommunity structure. Instead, spatial extent (i.e., the total area of observation encompassing all observation units) and grain (the area of the observation unit) of sampling are often chosen arbitrarily based on logistics and/or features of the landscape. For example, the studies included in syntheses by Cottenie (2005) and Soininen (2014, 2016) were based on data collected over widely different spatial extents and grains. If spatial scale influences conclusions about the relative importance of different assembly mechanisms, it would be critical to recognize, and account, for this relationship.

One way that scale can influence the importance of community assembly mechanisms is via increases in spatial extent, which will typically increase the magnitude of habitat heterogeneity encompassed by the study. As a result, systems that may appear more neutral when observed at smaller scales can appear more niche-structured at larger scales (e.g., Chase 2014). For example, Garzon-Lopez et al. (2014) analyzed the distributions of several tree species on Barro Colorado Island, Panama. When they observed species distributions at the scale of the 50-ha permanent forest plot that serves as a “type case” of a largely neutrally structured community (e.g., Hubbell 2001, Condit et al. 2012), they found little association with habitat characteristics. However, when they increased the window of observation to encompass more heterogeneity across the entire island, those same tree species distributions become more strongly habitat-associated. Likewise, the relative importance of dispersal limitation and stochasticity may increase at larger spatial extents, possibly at the cost of niche selection if species are not able to track suitable habitat across the whole extent (e.g., Ng et al. 2009, Declerck et al. 2011).

Sampling grain can also sway inference of community assembly processes. As the sampling grain increases, the number of individuals and species increase while the location and environmental variables are averaged within the sampled plot. We might expect that when the grain of observation is significantly coarser than the grain of environmental variation, the relative importance of environment for explaining community structure will decrease.

These scaling issues beg for a shifting paradigm in the type of question we ask in community ecology. For example, rather than simply asking about the relative importance of niche selection processes, dispersal and/or drift (e.g., Vellend 2010, 2016), we argue that this question must be put in a scale-explicit context. In what follows, we systematically explore how sampling extent and grain alter our inference of assembly processes. To do so, we describe the variation in the type and shape of the relationships between sampling grain and sampling extent, and the relative importance of niche selection relative to dispersal and drift in explaining diversity patterns (hereafter called “scaling relationship”).

Our basic approach consisted of (1) simulating community assembly under a predefined set of rules that produce a continuum between neutral and niche-based processes; (2) sampling the simulated communities across spatial extents and using different sampling grains; and (3) analyzing data using standard statistical tools to infer community assembly processes (Fig. 1). We show how increasing sampling extent leads to inference of stronger niche selection, whereas increasing sampling grain leads to inference of weaker niche selection. Further, we characterize the shape of the scaling relationship and illustrate how we can derive a parametric scaling coefficient that describes its shape. Finally, to contextualize the importance of the scaling effects, we compare our results to a broad range of metacommunities sampled in the context of syntheses by Cottenie (2005) and Soininen (2014). In doing so, we assess to what extent sampling effects can reproduce some of the empirical variation observed that would otherwise be interpreted as differences in the relative importance of assembly processes.

METHODS

Simulating community assembly

We used an individual-based model on a lattice, where only one individual could occupy a given cell. Although model rules were designed to be as general as possible, it resembles the lottery model of Gravel et al. (2006) and extensions of it (e.g., Lasky and Keitt 2013, Latombe et al. 2015) parameterized in line with dynamics of forest communities. This model was chosen due to its simplicity and utility for varying both grain and extent to analyze community assembly outcomes. We built the model to flexibly simulate a continuum between neutral and niche dynamics by varying dispersal limitation and niche differentiation, creating a trade-off between stochastic and

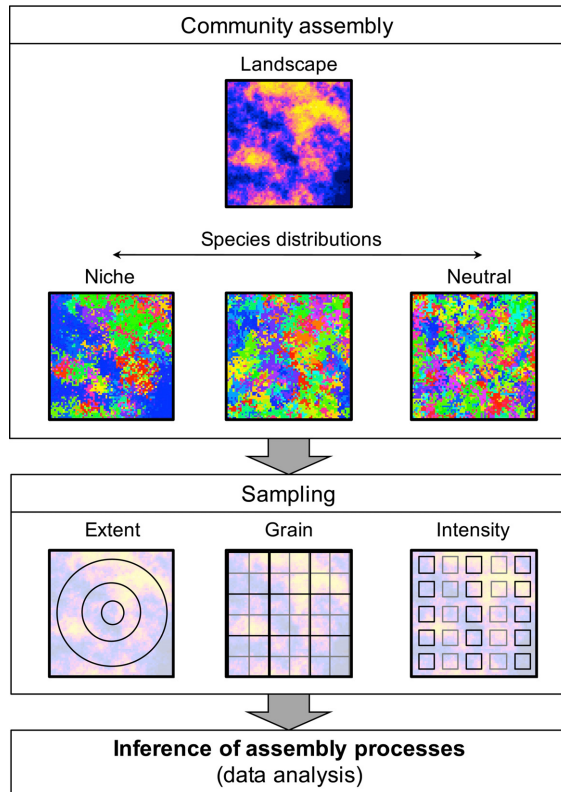


FIG. 1. Methodological framework used to explore scaling effects on the inference of community assembly processes.

competitive exclusion. Pure neutral dynamics emerged when we assumed a degree of dispersal limitation and total niche overlap (i.e., functional equivalence) between species, whereas pure species sorting was possible under complete niche differentiation.

We simulated community assembly on landscapes composed of one environmental variable simulated according to a Gaussian random field with autocorrelation defined by the “range” parameter (see examples in Appendix S1: Fig. S1). Simulations consisted of four basic processes: reproduction, mortality, dispersal and colonization. Neutral dynamics were simulated with random reproduction (randomly chosen reproducers), death and colonization, while species under selection scenarios were characterized by a fundamental Gaussian niche that defined their performance in a given environment (λ_i) as

$$\lambda_i(E) = \exp\left[\frac{-(E - \mu_i)^2}{2\sigma^2}\right]$$

where E is the environmental value, μ_i is the optimal environmental condition for species i (i.e., the trait value) and σ is the fundamental niche breadth (equal for all species; Tilman 2004, Gravel et al. 2006). λ_i determined the probability of survival, reproduction, and colonization in environment E . Dispersal was limited only

by distance according to a lognormal kernel $W(r)$, where the location parameter ($\mu_{\text{dispersal}}$) was 0 (i.e., dispersal peaks at a distance of one grid cell) and the scale parameter ($\sigma_{\text{dispersal}}$) controlled the dispersal capacity. Such a lognormal dispersal kernel has been found in many seed dispersal systems (Rawsthorne et al. 2009, Viana et al. 2013). In addition to dispersal within the grid, we incorporated immigration (m) from outside the grid (i.e., from the metacommunity) to avoid long-term monodominance in communities that were more neutral. The immigration rate was defined as

$$m = \frac{Pr_m}{\pi A}$$

where P is the perimeter of the grid, r_m is the mean distance between adult and recruit, and A is grid area (Chisholm and Lichstein 2009). The values for all parameters can be found in Appendix S1: Table S1.

In each time step (one generation), (1) a given proportion of individuals in the landscape died according to the defined mortality rate (0.02; rounded up from 0.013 [Condit et al. 2006] to accelerate dynamics), (2) a given proportion of individuals reproduced (0.7; Wright et al. 2005) by producing 10 dispersing propagules each (corresponding to the lower limit of sapling density found in temperate forests; Pacala et al. 1996), (3) the propagules dispersed in a random direction and over distances sampled from the dispersal kernel, and finally (4) the propagules colonized empty cells. Whenever more than one propagule arrived in the same cell, individuals competed where the winning probability was λ (under neutrality, this probability was equal). The recruitment probability R_i for species i in a given empty cell is the sum of its propagules produced by N conspecific adults located at r distances, weighted by the dispersal function $W(r)$, divided by the sum of the propagules coming from adults of all j species at all r distances (Gravel et al. 2006). Because we also defined a fixed immigration rate m (with equal probability for all species), the recruitment probability is

$$R_i = (1 - m) \frac{\sum_{r=1}^n \lambda_i N_{i,r} W(r)}{\sum_{j=1}^S \sum_{r=1}^n \lambda_j N_{j,r} W(r)} + m.$$

We ran 10 replicate simulations for each parameter combination to account for variation resulting from stochastic community assembly.

Sampling of simulated communities

We varied the spatial extent of sampling by choosing one origin cell randomly across the grid and sampling all cells within progressively increasing circular areas from the origin (10 origins were chosen to replicate sampling). For grain size, the optimal grain size should be equal to the environmental grain, that is, to the maximum area within which the environment is homogeneous. Thus, to

explore grain effects, we first ran the simulation model on “patchy” landscapes with homogeneous environmental conditions within patches and used a sampling grain that corresponded exactly to the patches. Next, we increased grain size by progressively decreasing the number of equal-sized sampling plots into which the whole extent was divided. This compact stratification was performed by means of *k*-means clustering using the R package *spcosa* (Walvoort et al. 2010), where the grid is partitioned according to a classification scheme based on the geographical coordinates of grid cell midpoints that are iteratively reallocated to clusters to minimize the mean square shortest distance.

Inference of the relative importance of assembly processes

As discussed above, the most popular method for inferring the relative importance of community assembly processes, despite its limitations, remains partitioning the compositional variation explained by (groups of) predictors such as spatial and environmental variables (Borcard et al. 1992, Peres-Neto et al. 2006). This approach is, however, based on linear regression and is thus limited if species respond nonlinearly to the environment, such as when niches are Gaussian (a pervasive pattern in nature). Adding higher-order polynomials could be a solution to model non-linear relationships, but the typical large number of zeros (i.e., species absences) is not appropriately accommodated with available methods. For this reason, and to isolate and illustrate the effect of scale, we used the trait values of the species (i.e., μ_i) as the response variable in a simple linear regression model. In a scenario of perfect species sorting (i.e., under complete niche differentiation), the match between μ_i and the environment would be perfect and the coefficient of determination (R^2) would be 1. If species cannot fully track the environment, either because their niche overlaps with other species (generating competition for the resource), because of dispersal limitation, or because of stochasticity, the R^2 decreases. More complex approaches involving a species abundance matrix as a response variable could be applied to the same set of simulations, but would not change our main conclusions.

In order to account for dispersal limitation, we added spatial variables created by means of Moran’s Eigenvector Maps (MEM) as predictors to the linear model (Dray et al. 2006). Thus, we evaluated the relative importance of selection, dispersal, and drift by partitioning the variation attributed to the effects of the environment [E] and space [S] plus unexplained variation [R], respectively. Because cells are regularly distributed and the environment is (to some degree) spatially correlated, the MEM variables efficiently captured the spatial structure of the environment. Thus, we interpreted the shared variation fraction between the environment and space [E∩S] as being driven by the effect of the environment, and the unique contribution of [S] as dispersal limitation. We acknowledge that in the special case where the scale of environmental autocorrelation

matches the scale of intraspecific aggregation resulting from dispersal limitation, there is some chance of inferring spurious habitat associations (Smith and Lundholm 2010). Still, using trait values rather than species abundances should limit spurious habitat associations arising from dispersal-mediated aggregation.

Finally, we evaluated whether stochastic processes could generate spatial patterns that could influence our interpretation of the shared and spatial variation fractions. We performed 1,000 stochastic simulations of neutral dynamics with no dispersal limitation and found only a small percentage of simulations with a significant spatial pattern (5.1%, $P < 0.05$), with the proportion of explained variation never exceeding 0.064 (median < 0.005). After partitioning the variation, the maximum explained by the shared fraction (between space and environment) was negligible (0.002). Therefore, in ~5% of our simulations reported below, a small proportion of variation in the exclusive spatial fraction might be explained by pure stochasticity, but did not affect the relative importance of niche selection.

The scaling relationship

To investigate how the relative importance of niche selection varies as a function of spatial extent and grain of sampling, we characterized the shape of the relationship between the fraction of variation explained by the environment (i.e., the partitioned R^2 resulting in fraction [E]) and either spatial extent or grain. By fitting a regression model to the scaling relationship, we estimated a parametric scaling coefficient, which was used as a scale-integrative measure of the relative importance of niche selection. The scaling relationships were mainly driven by environmental heterogeneity, with [E] increasing linearly with environmental heterogeneity regardless of landscape configuration (see *Results* and Appendix S1: Fig. S2). The linear trend of this scaling relationship was robust across simulated landscape configurations and community dynamics, but further exploration with empirical data is needed to confirm the generality of this form. To avoid effects of landscape configuration such as those derived from gradient and mosaic landscapes (see *Results*), we measured environmental heterogeneity as mean Euclidean distance in environment, rather than spatial scale, as the “scaling” factor. This provides a more universal scaling factor, not only because of landscape configuration, but also because relevant scales of environmental variation differ among taxa; for example, macroorganisms are responsive to environments structured over larger spatial scales than microorganisms.

RESULTS AND DISCUSSION

Sampling extent

The relative importance of the environment in explaining community composition [E] increased logarithmically

with increasing sampling extent whenever species had some degree of niche differentiation (Figs. 2 and 3). However, landscape configuration affected the scaling relationships (Fig. 2a–c). In gradient landscapes where the environment varies more linearly (see Appendix S1: Fig. S1), the scaling relationship tends to conform to a logarithmic pattern (Fig. 3a). However, in mosaic landscapes (see Appendix S1: Fig. S1), the scaling relationship is affected by the scale at which the environment is repeated across space. Both niche breadth and dispersal capacity affected the scaling relationship (Fig. 3a–c). The scaling coefficient decreased from higher to lower niche differentiation (Fig. 3a, c), becoming null under virtually neutral communities. Finally, species' dispersal capacity affected the scaling relationship: under selection, low to intermediate dispersal capacity led to higher coefficients compared to very low and high dispersal (Fig. 3b, c). At high dispersal capacity, the results were consistent with a mass effects scenario (Fig. 3c), in which species with lower performance in given environments could nevertheless persist due to spillover (Mouquet and Loreau 2003, Matias et al. 2013).

Sampling grain

In general, the relative importance of the environment in explaining community composition [E] decreased with

increasing sampling grain (Figs. 2 and 3). However, these scaling effects were stronger in mosaic landscapes as compared to gradient landscapes and were larger for the intercept rather than the slope of the scaling relationship. Larger ranges of environmental autocorrelation led to slightly higher intercepts (Fig. 2d, e), and the slope of the relationship was more affected in mosaic than in gradient landscapes (Fig. 2f). On the other hand, larger dispersal capacity and niche breadth strongly decreased the intercept (Fig. 3d, e) and, to a lesser degree, the slope of the scaling relationship (i.e., the slopes were more negative; Fig. 3d–f).

Contextualisation of scaling effects

The results from our simulation modeling show that inference of community assembly processes strongly depends on sampling grain and extent. Thus, we hypothesize that the results of empirical studies are also affected by both the grain and extent of sampling in the study. We observed that in most scenarios where both neutral and selection processes act together, conclusions about the relative importance of the assembly drivers (selection, dispersal limitation, and drift) reverse with sampling extent (Fig. 4a). Importantly, this magnitude of variation observed across sampling extents even within a single set of simulation parameters is comparable to that observed across all empirical studies synthesized in Cottenie (2005)

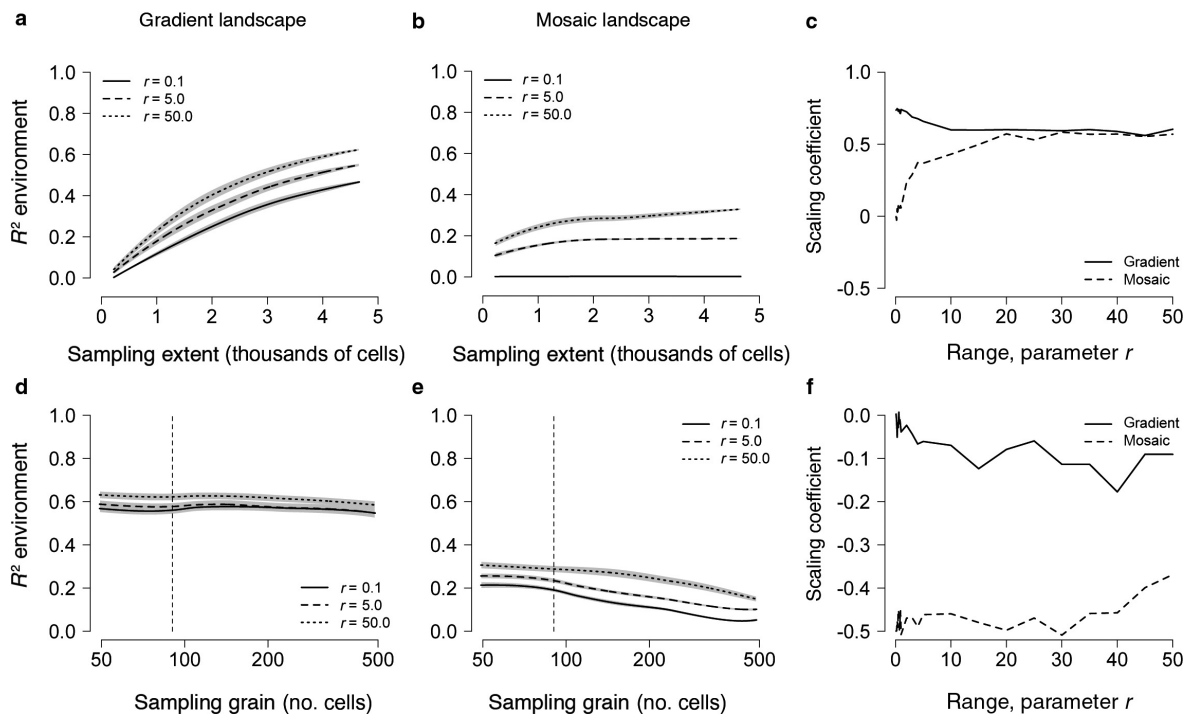


FIG. 2. Scaling effects generated by varying sampling extent and grain on the importance of the environment in explaining community composition (“scaling relationships”) under different landscape configurations: gradient and mosaic landscapes with different environmental autocorrelation (i.e., varying variogram range). The scaling coefficient in panels c and f results from the relationship between spatial scale (extent or grain) and the relative importance of the environment (niche selection). The scaling coefficient represents a scale-integrative measure of process importance.

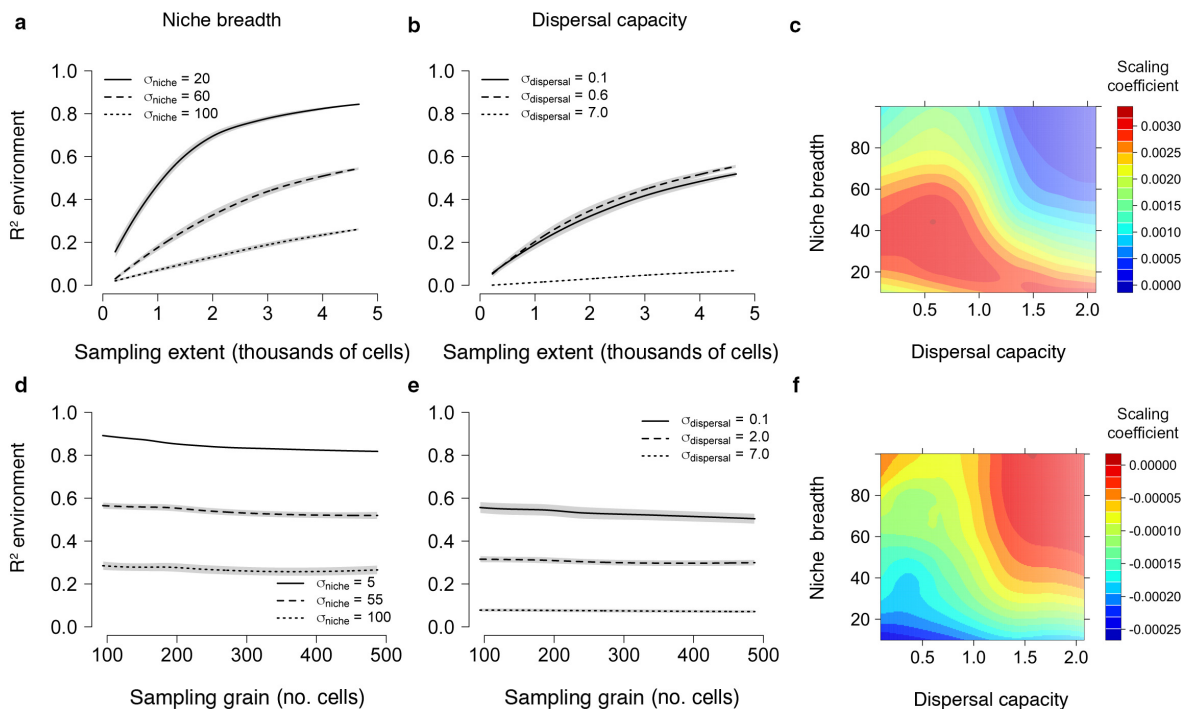


FIG. 3. Scaling effects generated by varying sampling extent and grain on the importance of the environment in explaining community composition ("scaling relationships") under different niche breadths and dispersal capacities, which produce variation along the neutral-niche continuum. Color in panels c and f represents the scaling coefficient of the relationship between spatial scale (extent or grain) and the relative importance of the environment (niche selection). The scaling coefficient represents a scale-integrative measure of process importance.

and Soinen (2014) (Fig. 4b). Specifically, the importance of selection increases with spatial extent in our simulations (R^2 increases from 0 to 0.60), and this was comparable with the variation observed in empirical studies (R^2 varies from 0.10 to 0.70). Likewise, as extent increases, the importance of dispersal decreases (R^2 from 0.60 to 0.20), which again is comparable to the empirical variation (R^2 ranges from 0.50 to 0.05). The effect of sampling grain is also important, though less in magnitude. Our ability to detect dispersal limitation decreased considerably with increasing sampling grain, which leads to the conclusion that selection was generally the most important driver (e.g., Fig. 4c), except when community assembly approached neutrality. Although less dramatic, we also see that varying sampling grain caused considerable variation, particularly in the inferred importance of selection, which ranged from an R^2 of 0.40 at fine grains to 0.10 at coarse grains, again spanning some of the range observed among empirical studies (Fig. 4d).

CONCLUSIONS, CAVEATS, AND FUTURE DIRECTIONS

Our main message is simple: sampling extent and grain have profound effects on the inference of community assembly processes, including many cases where differences in the scale of observation can reverse conclusions about the relative importance of selection,

dispersal and drift. It is clear that it is necessary to account for these scaling effects if we are to understand the relative importance of different metacommunity assembly processes in different places and times. We argue that only scale-integrative inferences can be useful to compare studies on different taxa, regions and ecosystems, and contribute to synthesis in community ecology.

Based on our results, we provide some recommendations regarding sampling and experimental designs. (1) Communities should be sampled over multiple spatial extents to progressively increase the environmental heterogeneity (i.e., increase the coverage of relevant environmental gradients) and respective species responses. This will allow an estimate of a scaling coefficient that is a quantitative measure of the relative importance of processes. The scaling coefficient can then be used to compare different (meta)communities in a scale-integrative manner. (2) Sampling grain size should be optimized to match environmental grain as closely as possible. Because environmental grain is multivariate, optimization requires choosing a grain size that maximizes environmental heterogeneity. Alternatives are to sample all individuals across space, which can be an expensive and daunting task (but see e.g., permanent forest plots; Condit 1995, Anderson-Teixeira et al. 2015), or simply to reduce sampling grain as much as possible. Finally, (3) the effort of sampling across different spatial extents at small grain sizes might be alleviated

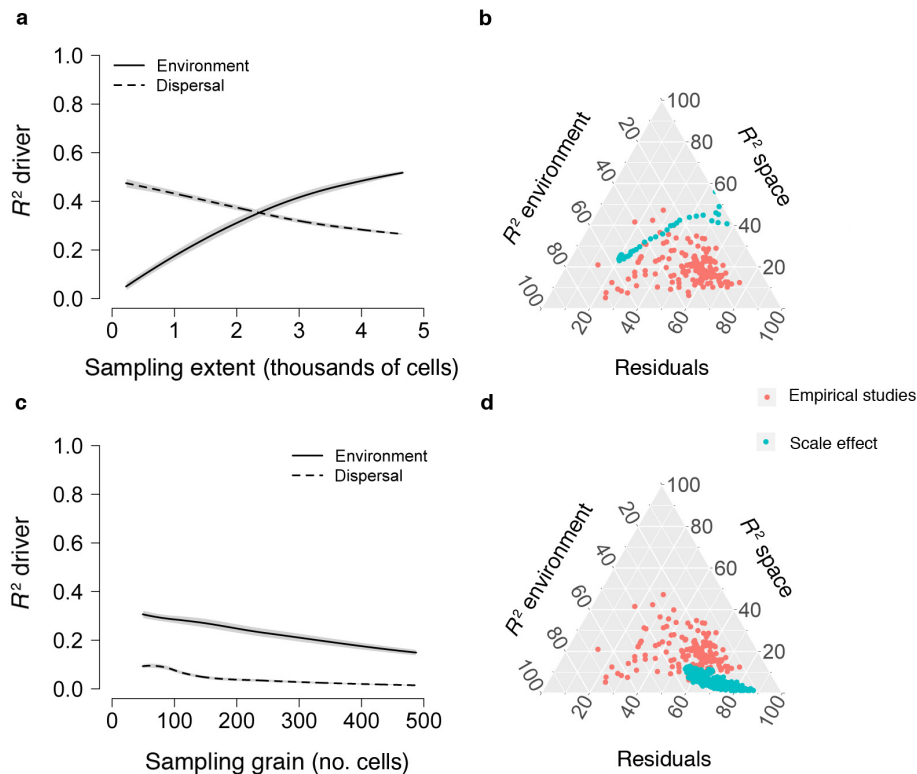


FIG. 4. Scaling effects (sampling extent and grain) on the inference of community assembly processes: niche selection, dispersal limitation, and ecological drift. Panels b and d show ternary plots representing the relative importance of the community assembly processes inferred (1) in different studies reviewed in Cottenie (2005) and Sojininen (2014) and (2) from one simulated community sampled over different spatial extents (b; model parameters: range = 25; $\sigma_{\text{niche}} = 60$; $\sigma_{\text{dispersal}} = 0.3$) and at different spatial grains (d; model parameters: range = 50; $\sigma_{\text{niche}} = 50$; $\sigma_{\text{dispersal}} = 1.0$).

to some extent by using a regular sampling configuration that maximizes environmental coverage.

The scaling relationships we illuminate here can also provide important context for conservation. This is because the scaling relationship detects the minimum extent at which environmental heterogeneity is needed to maintain diversity in the study area; that is, the extent at which the scaling relationship reaches an asymptote corresponding to the maximum compositional variation explained by the environment. This information might be useful, for example, if a goal is to restore disturbed habitats and maximize regional species diversity; the scaling relationship can be used to estimate the minimum area with sufficient environmental heterogeneity required to maintain the regional diversity.

Our simulations were limited to the extreme cases of environmental selection (niche) and dispersal and drift (neutral) processes. Our main intent was simply to illustrate how different aspects of scale can fundamentally influence our understanding and inference of the relative importance of different metacommunity assembly processes. However, communities consist of a multitude of other assembly processes, including intra- and interspecific competition (which can also be influenced by niche selection), patch dynamics, temporal dynamics and priority effects. The inference of these is also likely

sensitive to sampling scale. However, at the moment, we are largely unable to infer these processes because of a lack of appropriate analytical tools. If and when we are able to do so, it will also require explicit consideration of the sorts of scaling patterns discussed here.

Many analytical tools have been developed and used to infer community assembly processes, including pattern analysis (e.g., species abundance distributions), Mantel correlation tests, distance-based regressions (MRM, GDM) and multivariate statistics such as constrained ordination (e.g., CCA and RDA) and posterior variation partitioning. However, none of these methods are perfect and inferring processes from empirical data is still a challenge. Thus, while we advocate that the estimation of scaling coefficients is necessary to more accurately infer process, this will still critically depend on the use of appropriate statistical methods. New methods, such as joint species distribution models (e.g., Ovaskainen et al. 2017), seem promising. But these will almost certainly still require a scale-explicit approach to appropriately infer potential processes.

Overall, our study is a proof-of-concept towards a more scale-integrative approach in metacommunity ecology, but is certainly only a first step. The field of metacommunity ecology has been fostered by key conceptual advances, particularly the recognition that a number of processes, including those as seemingly diametrically

opposed as niche and neutral processes, play out simultaneously in metacommunities (Gravel et al. 2006, Vellend 2010, 2016, Fournier et al. 2017, Leibold and Chase 2017). However, available analytical methodologies to study and infer community assembly processes are not keeping pace and hamper our ability to synthesize knowledge. We now know that using only environment and space to infer complex and interacting assembly processes is not enough and that we need to integrate spatial scale, time, species covariance, and better descriptors of connectivity to fully understand community assembly mechanisms. Here, we have more explicitly described how the issue of spatial scale (both grain and extent) is critical to infer and understand community assembly processes, and we provide guidelines on how we can incorporate spatial scale into process inference.

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LITERATURE CITED

- Anderson-Teixeira, K. J., et al. 2015. CTFIS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* 21:528–549.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- Chase, J. M. 2014. Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science* 25:319–322.
- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* 159:1–23.
- Chisholm, R. A., and J. W. Lichstein. 2009. Linking dispersal, immigration and scale in the neutral theory of biodiversity. *Ecology Letters* 12:1385–1393.
- Chisholm, R. A., and S. W. Pacala. 2010. Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proceedings of the National Academy of Sciences USA* 107:15821–15825.
- Condit, R. 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10:18–22.
- Condit, R., et al. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.
- Condit, R., et al. 2006. The importance of demographic niches to tree diversity. *Science* 313:98–101.
- Condit, R., R. A. Chisholm, and S. P. Hubbell. 2012. Thirty years of forest census at Barro Colorado and the importance of immigration in maintaining diversity. *PLoS ONE* 7:1–6.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175–1182.
- Declerck, S. A. J., J. S. Coronel, P. Legendre, and L. Brendonck. 2011. Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography* 34:296–305.
- Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196:483–493.
- Fournier, B., N. Mouquet, M. A. Leibold, and D. Gravel. 2017. An integrative framework of coexistence mechanisms in competitive metacommunities. *Ecography* 40:630–641.
- Garzon-Lopez, C. X., P. A. Jansen, S. A. Bohlman, A. Ordonez, and H. Olf. 2014. Effects of sampling scale on patterns of habitat association in tropical trees. *Journal of Vegetation Science* 25:349–362.
- Gilbert, B., and J. R. Bennett. 2010. Partitioning variation in ecological communities: Do the numbers add up? *Journal of Applied Ecology* 47:1071–1082.
- Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences USA* 101:7651–7656.
- Gravel, D., C. D. Canham, M. Beaudet, and C. Messier. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399–409.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Lasky, J. R., and T. H. Keitt. 2013. Reserve size and fragmentation alter community assembly, diversity, and dynamics. *American Naturalist* 182:E142–E160.
- Latombe, G., C. Hui, and M. A. McGeoch. 2015. Beyond the continuum: a multi-dimensional phase space for neutral-niche community assembly. *Proceedings of the Royal Society B* 282:20152417.
- Layeghifard, M., V. Makarenkov, and P. R. Peres-Neto. 2015. Spatial and species compositional networks for inferring connectivity patterns in ecological communities. *Global Ecology and Biogeography* 24:718–727.
- Legendre, P., X. Mi, H. Ren, K. Ma, M. Yu, I. F. Sun, and F. He. 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90:663–674.
- Leibold, M. A., and J. M. Chase. 2017. *Metacommunity ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Matias, M. G., N. Mouquet, and J. M. Chase. 2013. Dispersal stochasticity mediates species richness in source-sink metacommunities. *Oikos* 122:395–402.
- May, F., A. Huth, and T. Wiegand. 2015. Moving beyond abundance distributions: neutral theory and spatial patterns in a tropical forest. *Proceedings of the Royal Society of London B: Biological Sciences* 282:20141657.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature* 422:881–885.
- Monteiro, V. F., P. C. Paiva, and P. R. Peres-Neto. 2017. A quantitative framework to estimate the relative importance of environment, spatial variation and patch connectivity in driving community composition. *Journal of Animal Ecology* 86:316–326.
- Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162:544–557.
- Münkemüller, T., F. de Bello, C. N. Meynard, D. Gravel, S. Lavergne, D. Mouillot, N. Mouquet, and W. Thuiller. 2012. From diversity indices to community assembly processes: a test with simulated data. *Ecography* 35:468–480.
- Ng, I. S. Y., C. M. Carr, and K. Cottenie. 2009. Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* 619:133–143.

- O'Neill, R. V., C. T. Hunsaker, S. P. Timmins, B. L. Jackson, K. B. Jones, K. H. Riitters, and J. D. Wickham. 1996. Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology* 11:169–180.
- Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, and N. Abrego. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters* 20:561–576.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625.
- Rawsthorne, J., D. A. Roshier, and S. R. Murphy. 2009. A simple parametric method for reducing sample sizes in gut passage time trials. *Ecology* 90:2328–2331.
- Shipley, B., C. E. Timothy Paine, and C. Baraloto. 2012. Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology* 93:760–769.
- Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1.
- Smith, T. W., and J. T. Lundholm. 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography* 33:648–655.
- Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95:3284–3292.
- Soininen, J. 2016. Spatial structure in ecological communities - a quantitative analysis. *Oikos* 125:160–166.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA* 101:10854–10861.
- Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* 299:241–244.
- Vellend, B. M. 2010. Conceptual synthesis in community ecology. *Quarterly Review of Biology* 85:183–206.
- Vellend, M. 2016. *The theory of ecological communities*. Princeton University Press, Princeton, New Jersey, USA.
- Viana, D. S., L. Santamaría, T. C. Michot, and J. Figuerola. 2013. Allometric scaling of long-distance seed dispersal by migratory birds. *American Naturalist* 181:649–662.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative abundance in ecology. *Nature* 424:1035–1037.
- Walvoort, D. J. J., D. J. Brus, and J. J. De Gruijter. 2010. An R package for spatial coverage sampling and random sampling from compact geographical strata by k-means. *Computers and Geosciences* 36:1261–1267.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385.
- Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21:307–315.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2576/supinfo>

DATA AVAILABILITY

Code is available on Zenodo: <https://doi.org/10.5281/zenodo.1484091>