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The effect of spatial configuration of habitat capacity on β diversity

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Abstract. Patterns of β diversity are commonly used to infer underlying ecological processes. In this study, we examined the effect of spatial configuration of habitat capacity on different metrics of β diversity, i.e., β diversity measured as turnover and as variation. For β diversity as turnover, a monotonic species spatial turnover pattern is typically considered as a benchmark for species distributions driven only by dispersal process. Deviations from a monotonic curve are attributed to local environmental filtering (i.e., the same environmental factors affecting different species differently). However, we found non-monotonicity in species spatial turnover in models without environmental filtering effect. This non-monotonicity was caused by variation in α diversity, introduced by spatial configuration of habitat capacity. After applying a recent null-model approach—designed to tease out the effect of variation in α diversity—species spatial turnover remained non-monotonic. This non-monotonicity makes it problematic to use species spatial turnover to infer the underlying processes for species distribution, i.e., whether it is driven by environmental filtering or dispersal processes. Spatial configuration of habitat capacity also influences landscape connectivity. Small-habitat capacity sites may constrain movements of organisms (i.e., dispersal) between sites supporting high capacity habitats. We showed that in a landscape where small-habitat capacity sites were located in positions important for dispersal (e.g., in the center as opposed to on the edge of a landscape) has a higher spatial variation of species composition, hence, higher β diversity. Ecologists who use different measures of β diversity should be aware of these effects introduced by spatial configuration of habitat capacity.

Key words: β diversity; habitat capacity; landscape connectivity; monotonicity; similarity indices; spatial configuration; species spatial turnover.

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INTRODUCTION

A burgeoning challenge in ecology is to distinguish among the many dimensions of species diversity. Increased scientific activity has centered on the study of beta (β) diversity—broadly defined as the variation in species membership among locales—because it provides a direct link between local biodiversity (α diversity) and regional species pool (γ diversity) (Whittaker 1960, 1972) and it has numerous implications for conservation (Olden 2006). Ecologists frequently use β diversity to infer processes that structure species assemblages spatially

(Vellend 2010). However, landscape heterogeneity, one aspect of which is manifested as spatial variation in habitat capacity (defined as the potential number of individuals a site can hold) among sites, can make it difficult to infer processes from observed β diversity patterns. Variation in habitat capacity introduces, among other things, differences in α diversity among sites via the simple effect of random sampling. As a result, variation in α diversity can generate spurious similarities or differences between locales, i.e., β diversity (Lennon et al. 2001, Koleff et al. 2003, Baselga 2007, Chase et al. 2011).

Beta diversity is expressed both in terms of species turnover and variation (Anderson et al. 2011). Species turnover refers to the rate of change in community structure along a given gradient, such as the distance decay relationship (DDR) describing decreasing taxonomic similarity with geographic distance (e.g., Qian and Ricklefs 2007, Brown and Swan 2010). Ecologists expect monotonic decay of species spatial turnover to occur when a system is predominantly controlled by dispersal limitation, whereas deviations from DDR (i.e., "peaks" and "valleys" in the species spatial turnover) indicate the importance of local environmental filtering on species occurrence (e.g., Condit et al. 2002, Anderson et al. 2013, Bogan et al. 2013). β diversity as variation is captured by Whittaker's original measures ($\beta_w = \gamma/\bar{a}$) or the mean dissimilarity index (such as Bray-Curtis and Sorensen dissimilarity index) among communities ($\bar{d} = \frac{1}{m}\sum_{i,j<i}d_{ij}$, $m = N(N-1)/2$ is total sample units; Anderson et al. 2011). Greater values indicate higher variation in species composition across space. In this study, we examine how the validity of the inferences about ecological processes based on different measures of β diversity may be compromised by the spatial configuration of habitat capacity in a landscape. We define spatial configuration of habitat capacity (hereafter SCHC) as the spatial arrangement of sites with different habitat capacities in a landscape.

Various methods exist to correct for the effects of variation in α diversity on estimates of β diversity. It should be noted that these effects relate to the dependence of β diversity on the differences of α diversity between sites within a system; and they are not the same as the effects arising from the differences of the mean α diversity (i.e., averaged across all sites within a system) between different systems. The latter issue is related to the comparability of β diversity measures among systems with different mean α diversity, and has been addressed by several authors (e.g., Jost 2007, Baselga 2010, Jost et al. 2010). Our study addresses the first issue: the dependence of β diversity on the differences of α diversity between sites within a system (e.g., Lennon et al. 2001, Koleff et al. 2003, Baselga 2007). Chase et al. (2011) recently developed a null-model approach, originally proposed by Raup and Crick (1979), to detect whether different species compositions among sites result from variation in α diversity or from other ecological processes (e.g., deterministic environmental filtering and stochastic dispersal). However, this approach was developed for a pair of local communities, and its effectiveness and validity when applied to all pairwise combinations of communities in a landscape have not yet been systematically investigated.

Spatial configuration of habitat capacity also influences landscape connectivity. For example, low capacity habitats in the landscape matrix may constrain movements (i.e., dispersal) between locations supporting high capacity habitats. Greater connectivity among habitats allows immigration from others sites to offset local extinction events, leading to higher α diversity but lower variability in community composition across the landscape (i.e., lower β diversity). By contrast, lower connectivity can isolate habitats, leading to lower α diversity but higher species turnover (i.e., higher β diversity; Hubbell 2001, Economo and Keitt 2010, Carrara et al. 2014). Although the influence of landscape connectivity for community composition is widely appreciated (Chase and Ryberg 2004, Chave and Norden 2007, Minor et al. 2009), few studies have considered the sole effect of habitat spatial configuration on β diversity.

In this paper, we examine how the quantification and interpretation of β diversity patterns are influenced by the spatial configuration of habitat capacity. Addressing this question through the analysis of empirical data is challenging because many known and unknown ecological processes are in operation. Therefore, we examined the effects of SCHC on β diversity patterns using

simulated landscapes that are free from the effects of environmental filtering. A set of communities comprised a metacommunity on this landscape, and we assumed that the locales that supported the communities differed only in their habitat capacity. As a result, species distributions—and the corresponding β diversity patterns—would be controlled solely by dispersal and not by differences in the ecological niche requirements of species.

The SCHC gives rise to spatial variation in α diversity, which subsequently affects β diversity patterns (Lennon et al. 2001, Koleff et al. 2003, Baselga 2007, Chase et al. 2011). If the influence of α diversity can be effectively removed, β diversity patterns should have the following properties in the hypothetical landscape free from the effect of environmental filtering (Fig. 1). First, β diversity as turnover should conform to the monotonic decay relationship describing how species similarity decreases with spatial distance. Second, β diversity, measured as either turnover or variation, should be statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. Although these two predictions may appear intuitive, it is unclear whether frequently used β diversity measures conform to these properties. We systematically investigated the effects of SCHC on the robustness of these two properties by implementing a neutral metacommunity model (see, e.g., Hubbell 2001, Muneepeerakul et al. 2008) in the no-niche hypothetical landscapes described above.

Methods

We systematically investigated the effects of SCHC on estimates of β diversity by applying a neutral metacommunity model (Muneepeerakul et al. 2008) in one-dimensional landscapes (e.g., such as a stream) with different spatial configurations of habitat capacity (Fig. 2). In the "uniform" configuration, all sites had identical habitat capacity. In the "gradient" configuration, habitat capacity increased linearly along a hypothetical gradient. In the "random-shuffle" configuration, we randomized the spatial distribution of habitat capacities along the gradient. In the "V-shaped" configuration, habitat capacity was set high at both ends and low in

the middle of the gradient; this is akin to a stream system in which the headwater receives much rainfall and the downstream end connects to a large river, while the middle reaches are intermittent streams (e.g., Bogan et al. 2013). In the "hump-shaped" configuration, habitat capacity was large in the middle and small at the two extremes of the gradient—akin to an edge effect such as the boundaries of a forest experiencing more external pressure than its interior. All five configurations had the same average habitat-capacity size of 514, and thus the same total habitat capacity. All configurations except for the uniform configuration were built from the same set of habitat capacities, but they were configured differently in space (Fig. 2). The biggest sample-size discrepancy (i.e., ratio of largest to smallest habitat capacity) in the four non-uniform configurations was about 20.

The metacommunity consisted of 30 local communities, with a distance between neighboring sites of 1 arbitrary distance unit. The dispersal kernel was assumed to be a two-sided exponential distribution

$$K_{ij} = Ce^{-L_{ij}/a}$$

where K_{ij} is the probability that an organism produced at site j arrives at site i after dispersal; C is a normalization constant to ensure that for every site j, $\sum_i K_{ij} = 1$, i.e., no organisms traveled out of the metacommunity. L_{ij} is the distance between two habitats, and a was the characteristic dispersal distance. At each time step, a randomly selected individual died and the resources that previously sustained that individual became available to sustain a new individual. With probability v, the diversification rate, the empty spot was taken up by a new species (the diversification rate is a per-birth rate and is due to speciation or to immigration of a new species from outside the metacommunity). With probability $1 - v$, the empty spot was occupied by a species already existing in the system. In the latter case, the probability P_{ij} that the empty spot in site i would be colonized by a species from habitat j was determined as follows:

$$P_{ij} = (1 - v)\frac{K_{ij}H_j}{\sum_{k=1}^{N} K_{ik}H_k}$$

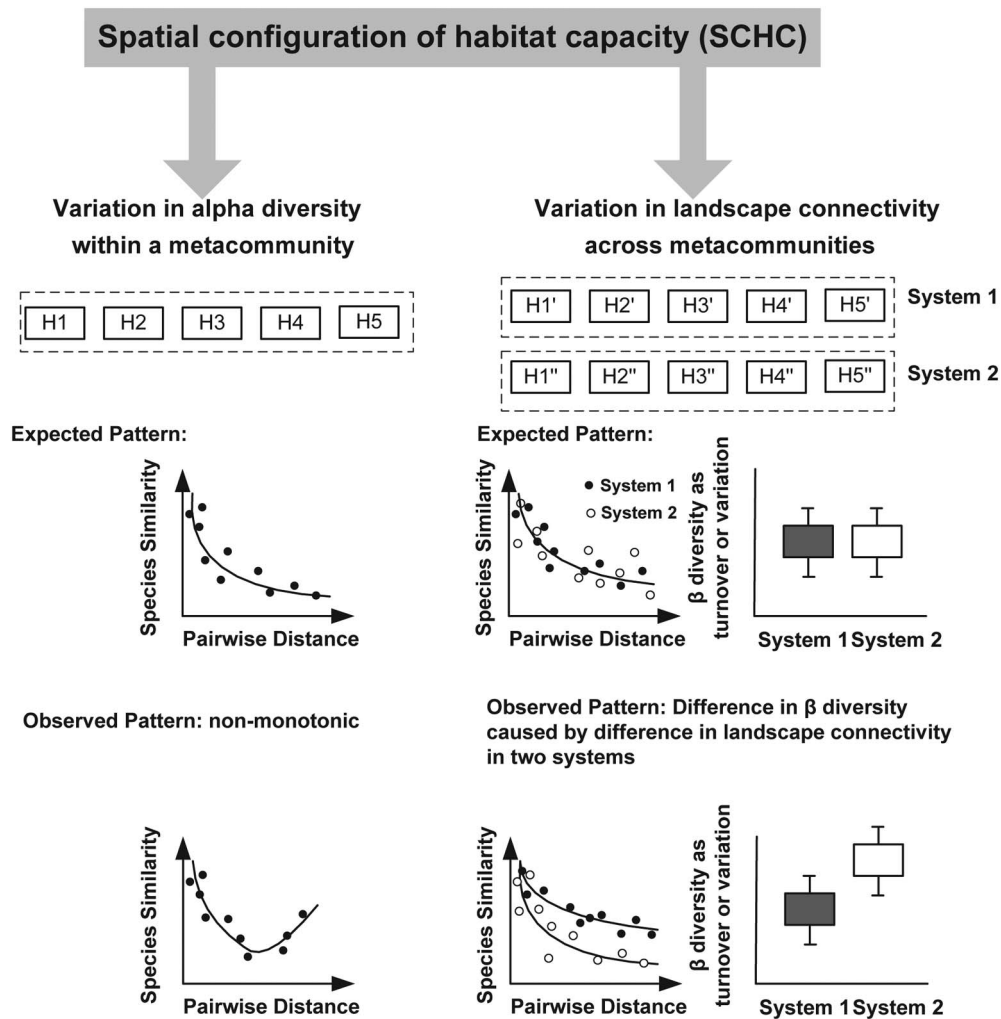where K_{ij} is the dispersal kernel, H_k is the habitat

Fig. 1. Schematic representation of the effect of spatial configuration of habitat capacity (SCHC) on β diversity—testing the validity of the two properties of β diversity when the metacommunity is controlled only by dispersal.

capacity of site k, and N is the total number of sites (i.e., communities). All the organisms in site j had the same probability of colonizing the empty spot at site i where the death took place. Each site was assumed to be always saturated at its habitat capacity.

We explored five characteristic dispersal distances ($a = 1, 4, 8, 12, 16$) at the diversification rate $v = 0.0010$. In the metacommunity's initial state, the distribution of species composition was random. We ran the model until it reached a statistically steady state (when there is no directional trend in the mean α diversity or total species richness with simulation time steps).

Results from the neutral metacommunity model were used to calculate different β diversity measures. Three commonly-used measures of β diversity were considered: Sorensen dissimilarity index based on species presence/absence data, Bray-Curtis dissimilarity index based on species abundance data, and the more recent Chao-Sorensen dissimilarity index based on species abundance data, which was originally created to address the issue of under-sampling rare species (Chao et al. 2005). For each configuration, we had 500 replicates (from 500 realizations of the same neutral metacommunity model) to calculate the mean and 95% confidence interval for each
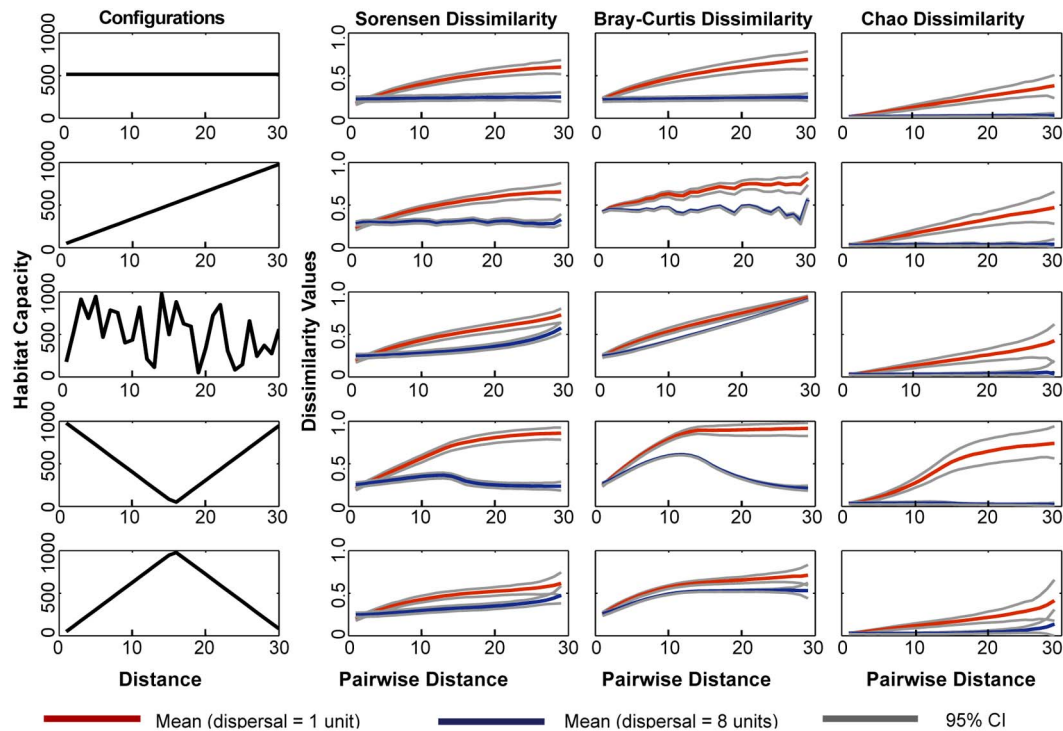
Fig. 2. Effect of spatial configuration of habitat capacity (SCHC) on species spatial turnover at two levels of dispersal limitation (solid red line: 1 distance-unit; solid blue line: 8 distance-units).

dissimilarity index at any particular pairwise distance.

Next, we tested the effectiveness of Chase et al.'s (2011) null-model approach, which was supposed to remove the effect of variation in α diversity. The calculated index is called pairwise β_{RC}. The β_{RC} metric expresses the magnitudes by which communities deviate from a stochastic null expectation. β_{RC} uses a randomization approach to estimate the probability of which pairwise communities have less observed number of shared species between two communities, containing α_1 and α_2 species respectively, than SS_{exp}. SS_{exp} is the expected number of shared species of a pair of communities by randomly drawing α_1 and α_2 species from a known species pool. The random draw was repeated 99,999 to create the SS_{exp} distribution. β_{RC} therefore calculates the probability that SS_{obs} is lower than SS_{exp} by chance (i.e., a dissimilarity index).

We used the four pairwise dissimilarity indices described above to calculate β diversity as turnover and as variation (Anderson et al. 2011). For β diversity as turnover, we used the slope between pairwise species similarity and pairwise geographical distance as a direct measure of turnover (e.g., Qian and Ricklefs 2007). We also considered the relative strength of the relationship (r^2) between species similarity and distance, as recommended by Anderson et al. (2011). To examine the non-monotonicity in the plot of species spatial turnover (x axis is pairwise distance, and y axis is dissimilarity index), we defined that if there exists a mean at larger pairwise distances statistically lower (Welch-Satterthwaite t test; $p < 0.01$) than a mean at smaller pairwise distance (meaning that species composition is more similar for the communities farther apart), it is considered to be non-monotonic. For β diversity as variation, we considered the classic metrics of β diversity, including Whittaker's proportional β diversity ($\beta_w = \gamma/\bar{a}$) and the additive model of β ($\beta_{Add} = \gamma - \bar{a}$; Lande 1996, Crist and Veech 2006), as well as multivariate measures of β diversity (i.e., the mean of the pairwise dissimilarity indices), which are based on pairwise resemblance of species among habitats (Ander-

son et al. 2011). Since the classic β diversity is directly derived from α and γ diversity, we investigated the effects of SCHC on α and γ diversity as well.

RESULTS

SCHC introduces non-monotonicity to species spatial turnover

By design, a neutral metacommunity model is free from the effects of environmental filtering, and thus patterns of spatial species turnover are shaped solely by stochastic dispersal. Therefore, we expect monotonic decay in species similarity with pairwise distance (or monotonic increase in species dissimilarity with pairwise distance; Fig. 1); however, we found little evidence for this relationship (Fig. 2). Species turnover was non-monotonic when measured by the traditional presence/absence-based Sorensen index and the abundance-based Bray-Curtis index (Fig. 2). Chao index, however, showed less evidence for non-monotonicity in species spatial turnover across different configurations (Fig. 2). The non-monotonicity observed was caused by the variation in α diversity among the communities induced by the SCHC.

The null model approach is not effective in separating α from β diversity

Next, we tested the effectiveness of Chase et al.'s (2011) method to disentangle α from β diversity in spatially explicit context. We tested this method in two steps. First, we tested it using a randomly assembled metacommunity without dispersal limitation. The dispersal-free metacommunities were created by randomly selecting species from a common pool of a given regional diversity ($\gamma = 200$). Each species had the same probability of being selected and was assigned to local communities until the local habitat capacity was reached. The random assembly of species was repeated 500 times for each configuration. Our results demonstrated two main findings. First, the mean pairwise similarity across 500 realizations was 0, indicating no difference from a random assemblage (Chase et al. 2011). Second, the slope of turnover curve was 0, with an intercept of 0 (Fig. 3). These results suggest that the Chase et al. (2011) method was effective under random species assemblages, i.e., no

dispersal introduced. It is worth noting that the confidence intervals were of varying widths, but all were wide (Fig. 3).

In the second step, we included dispersal limitation in creating metacommunities at landscapes of different SCHCs, and expected that β_{RC} would exhibit a monotonically increasing pattern in all configurations. Contrary to our expectation, in the hump-shaped and gradient configurations, we found that species turnover was non-monotonic (Fig. 3). We also found that the confidence interval generally became wider with increasing pairwise distance. Despite the widening confidence intervals, the non-monotonicity in species turnover curve was still statistically significant (Fig. 3).

SCHC causes differences in β diversity across metacommunities

We assessed the effect of SCHC on β diversity across metacommunities to determine whether, after correcting the effect of α diversity by Chase et al.'s (2011) method, β diversity is statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. To do this, we examined both types of β diversity: turnover and variation (Anderson et al. 2011).

We found that the slope between species similarity and geographical distance differed among varying configurations of the landscape (Figs. 2 and 3), and Chao index and β_{RC} did not conform to the linear models (i.e., very low r^2 values when the relationship was non-monotonic). We found that Whittaker's β_W and Lande's β_{Add} were also influenced by SCHC (Table 1, Fig. 4). Mean pairwise dissimilarity indices were also significantly different across configurations (Table 1, Fig. 4). Higher values were found in the V-shaped configuration and lower values in the hump-shaped configuration (Fig. 4). We also found that SCHC caused differences among metacommunities in both mean α diversity and γ diversity, especially in mean α diversity (Table 1, Fig. 4). Mean α diversity was much higher in the hump-shaped configuration than in the V-shaped configuration (Fig. 4). By contrast, mean γ diversity was slightly lower in the hump-shaped configuration than in the V-shaped configuration (Fig. 4).
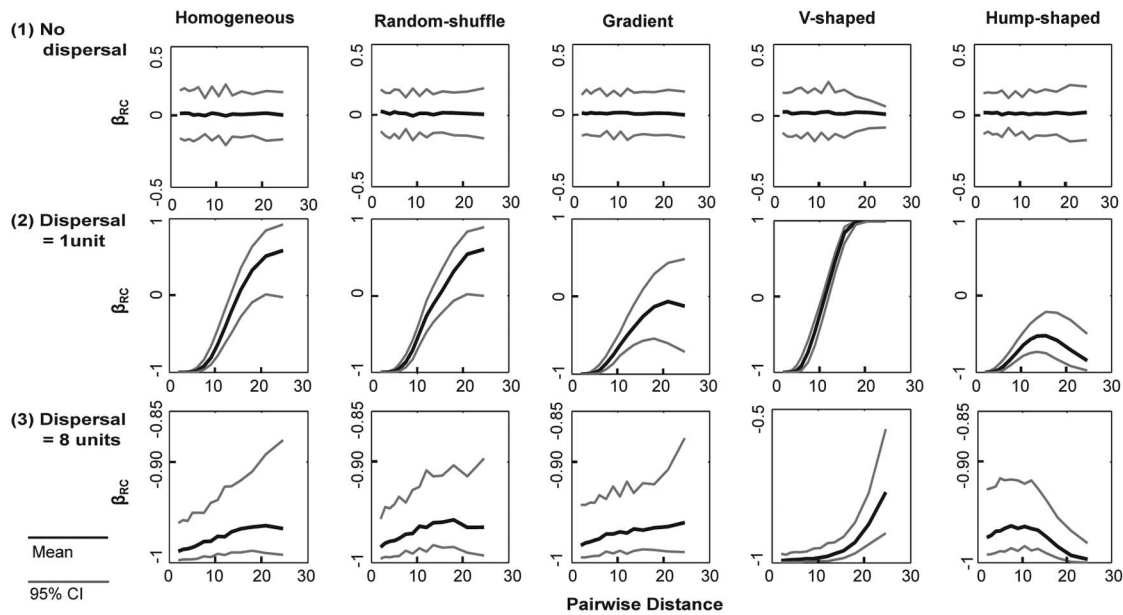
Fig. 3. Patterns of β_{RC} at different levels of dispersal distance (no dispersal, dispersal distance = 1 unit and 8 units; γ diversity = ~200).

Dispersal limitation changes the effect of SCHC

We examined two effects of SCHC: (1) its effect on the *shape* of species turnover curve (i.e., whether it is monotonic), and (2) its effect on the *value* of β diversity, both as variation and turnover, across metacommunities (Fig. 1). Both effects varied with the strength of dispersal limitation (Table 1, Figs. 2 and 3). Non-monotonicity was more evident when dispersal was more widespread according to the three traditional indices (Fig. 2). For β_{RC}, which corrects for α diversity variation, SCHC had greater effects on the shape of species turnover when dispersal was more local (Fig. 3). When dispersal limitation was absent, the shape of species turnover across different configurations was similar (Fig. 3), suggesting little effect of SCHC. In terms of SCHC's effect on β diversity across metacommunities, the influence of SCHC was more pronounced when dispersal was more local (Table 1), i.e., the difference in β diversity among metacommunities caused by SCHC is amplified when the dispersal was more local. We explored five levels of dispersal limitation, but only reported result for two; all the patterns reported here hold for the rest three dispersal levels.

DISCUSSION

The interdependence of β and variation in α

Table 1. Effects of the spatial configuration of habitat capacity (SCHC) measured by F (3, 1996) values on β diversity, mean α diversity, and γ diversity at two levels of hypothetical dispersal. The smallest F (3, 1996) value was 6.3, when ** $P = 0.003$. All other F values were greater than that, hence, much more significant effect of SCHC.

Dispersal levels	Multivariate measure of β as variation				Classic measure of β		α and γ	
	Sorensen	Bray-Curtis	Chao	β_{RC}	β_{Add}	β_W	Mean α	γ
1-unit	4806.4	9822.0	5357.1	7366.6	194.7	3330.3	2509.6	76.5
8-unit	13.8	89.5	6.3	194.8	130.0	1387.0	1158.0	45.7

Notes: For each configuration (total four different configurations, not including homogeneous configuration), 500 replicates (i.e., 500 realizations of the neutral metacommunity model) were used. γ diversity = ~200.
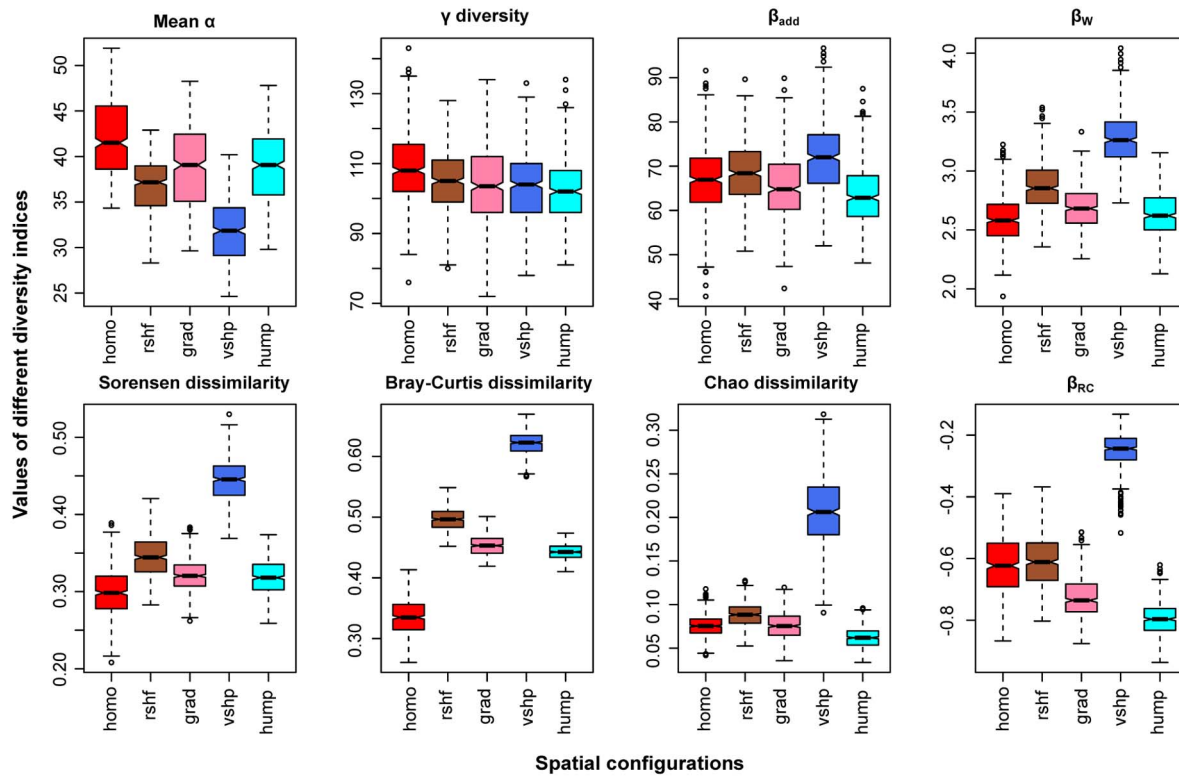
Fig. 4. The influence of SCHC on β diversity as variation, measured by classic metrics of species diversity (mean α, γ, β_{Add}, and β_w) and mean of dissimilarity indices (Sorensen dissimilarity index (SDI), Bray-Curtis dissimilarity index (BCI), Chao dissimilarity index, and β_{RC}). The results were based on 500 realizations of the neutral metacommunity model with a characteristic dispersal distance of 1 unit.

diversity is well established in the literature (e.g., Koleff et al. 2003, Jost 2007, Chase et al. 2011). One contribution of our study is to examine how spatial configuration of habitat capacity may affect different measures of β diversity in spatially explicit context, beyond just one pair of communities, through its influence on the variation in α diversity. We found that traditional similarity indices, be they incidence- or abundance-based were highly sensitive to the SCHC (Fig. 2). Even with only dispersal limitation in the model, patterns of species turnover measured by these indices were non-monotonic. Non-monotonicity, such as "peaks," "valleys," and "plateaus" (e.g., Condit et al. 2002, Anderson et al. 2013, Bogan et al. 2013), in species spatial turnover has been used as evidence for local environmental filtering processes shaping community composition and distribution. We did not observe non-monotonicity in the species spatial turnover

measured by Chao index (Fig. 2). Our findings imply that, when local habitat capacities in the landscape are not uniform (a common occurrence), analyses of spatial turnover based on these frequently used similarity indices should be interpreted with care because they are at risk of inadvertently conflating ecological processes with confounding effect by α diversity in their conclusions.

The methods available to remove the influence of α diversity variation seem ineffective for the β diversity patterns discussed here. For example, Chase et al.'s (2011) null-model approach, which was designed specifically to correct for the effect of variation in α diversity on β diversity, is useful for deciding whether the community assemblage is significantly different from a random assemblage. But it was developed for a single community pair; our results show that it is not readily transferable for comparisons among all pairs at
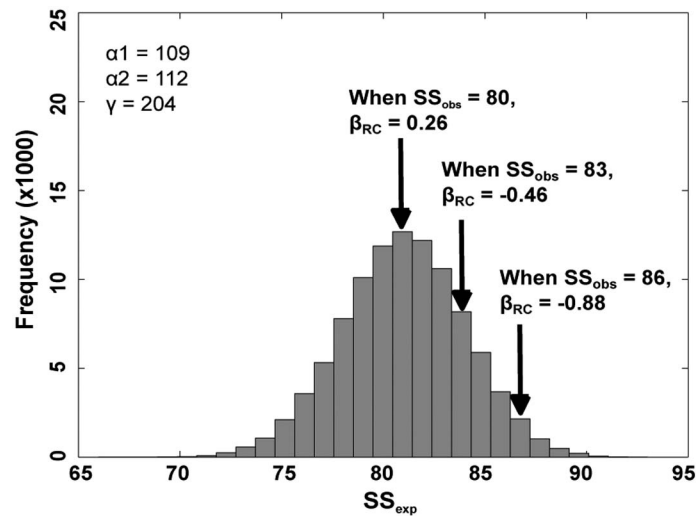
Fig. 5. Sensitivity of β_{RC} to small changes in observed shared species (SS_{obs}) when the value of SS_{obs} falls within or near the peak of SS_{exp} distribution. SS_{exp} distribution was created by 99,999 repeated random draws of α_1 and α_2 species from a known species pool. The γ diversity of 204 was taken from one of the neutral metacommunity model realizations in the V-shaped configuration with dispersal distance of 8 units.

landscape scales (Fig. 3). Nonetheless, β_{RC} has already been applied at landscape scales in many very recent studies (e.g., Akasaka and Takamura 2012, Bernard-Verdier et al. 2012, Anderson et al. 2013, Siepielski and McPeek 2013).

Why can't β_{RC} be extended to more than one pair? The calculation of β_{RC} is based on comparing the value of SS_{obs} with the probability density distribution of SS_{exp}. The probability density distribution of SS_{exp} is generated by repeated random sampling for a pair of communities with given α diversity levels. Inevitably, α diversity levels vary across different community pairs. Different α diversity combinations result in different shapes of the SS_{exp} distribution (i.e., skewedness and variance; Chase et al. 2011). Variation in the shape of SS_{exp} distribution makes comparison among different pairs problematic.

We note that β_{RC} is highly sensitive to SS_{obs}. When SS_{obs} falls near the peak of SS_{exp} distribution, a small change in the value of SS_{obs} results in a disproportionally large change in the value of β_{RC} (see Fig. 5 and its caption for an example)—even a change in its sign. In reality, under-sampling of rare species could easily result in such small fluctuations in the value of SS_{obs} collected in the field. Therefore, β_{RC} are not reliable for inferring underlying ecological pro-

cesses. To demonstrate this problem, we took two pairs of communities in the hump-shaped configuration as an example (Fig. 6). The first pair consists of the two communities at both ends (i.e., communities 1 and 30), and the second pair consists of communities 12 and 18, which are much closer to each other than the first pair. After removing the effect of variation in α diversity, we expected the second pair to be more similar in species composition, i.e., having a lower β_{RC}; instead, it was less similar (Fig. 6). Accordingly, this could lead to an interpretation that ecological processes other than dispersal are at play where there is none.

Another reason that SCHC causes complications in interpreting β diversity patterns is the spatial autocorrelation between the SCHC and dispersal. It is useful to see this through a lens of the effects of variation in habitat capacity. The variation in habitat capacity affects patterns of spatial turnover in two ways. First is a random sampling effect: if the overall species richness is fixed, two habitats with larger and more equal carrying capacity are likely to have a greater proportion of common species, hence a higher similarity value. Second is the spatial correlation between SCHC and dispersal. Corrective methods such as null-model shuffling (Kraft et al.
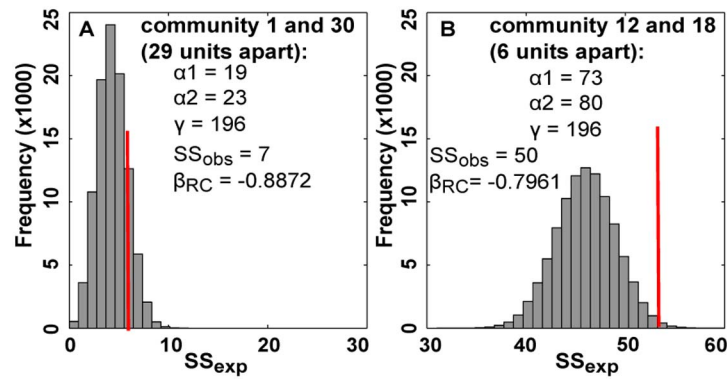
Fig. 6. Influence of the shape of SS_{exp} distribution on β_{RC}. The two pairs of communities shown are from the same neutral model realization: (A) the pair of communities with 29 units apart; and (B) the pair of communities with 6 units apart. Red bars indicate the number of observed shared species.

2011) effectively remove the random sampling effect, but not the spatial autocorrelation effect. Therefore, the effectiveness of these methods depends on species' dispersal capacity, which is difficult to estimate in reality, consequently, difficult to correct.

Another contribution of our study was that we confirmed the effect of SCHC on β diversity via its effect on landscape conductivity. The hump-shaped landscape and V-shaped landscape have same total habitat capacity; however, in the V-shaped landscape, the sites with lower habitat capacity level are located in the center of the landscape, and these lower-habitat-capacity sites are located on the edge of the landscape in the hump-shaped landscape. Smaller habitat capacity in the center of the landscape greatly reduces landscape connectivity, similar to bottleneck effect, and increases isolation among sites. As a result, the local species diversity is low (low mean α diversity), but the species composition is more spatially variable, i.e., higher β diversity (Fig. 4). By fixing the overall landscape carrying capacity, and only changing the spatial arrangement of habitats of different size, we demonstrated the significant effect of SCHC on different measures of β diversity. This mechanism is often neglected in interpreting β diversity patterns.

As the upshot of our investigation, we recommend that for ecologists who wish to use the shape of species spatial turnover to infer underlying ecological processes, Chao index is currently the best choice. According to our study, Chao index is considerably more robust than tradition-al similarity indices: it exhibits no or very weak non-monotonicity when only dispersal limitation is present. One possible explanation for this robustness is that SCHC influences spatial patterns of rare species, and the Chao index was already designed to minimize sensitivity to rare species (Chao et al. 2005). That said, the Chao index is not completely insensitive to the SCHC effects (Fig. 2). Our findings suggest that when inferring ecological explanations from β diversity patterns, researchers should take into account not only the commonly considered deterministic and stochastic processes (e.g., species adaption to habitat quality, dispersal, extinction, and speciation), but also the effects of spatial configuration of habitat capacities, which alters patterns of β diversity by introducing variation in α diversity and influencing landscape connectivity, which further influences dispersal limitation and other spatial processes.

Acknowledgments

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