

Differentiating between niche and neutral assembly in metacommunities using null models of β -diversity

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The β -null deviation measure, developed as a null model for β -diversity, is increasingly used in empirical studies to detect the underlying structuring mechanisms in communities (e.g. niche versus neutral and stochastic versus deterministic). Despite growing use, the ecological interpretation of the presence/absence and abundance-based versions of the β -null diversity measure have not been tested against communities with known assembly mechanisms, and thus have not been validated as an appropriate tool for inferring assembly mechanisms. Using a mechanistic model with known assembly mechanisms, we simulated replicate metacommunities and examined β -null deviation values 1) across a gradient of niche (species-sorting) to neutrally structured metacommunities, 2) through time, and 3) we compared the effect of changes in assembly mechanism on the performance of the β -null deviation measures. The impact of stochasticity on assembly outcomes was also considered. β -null deviation measures proved to be interpretable as a measure of niche or neutral assembly. However, the presence/absence version of the β -null deviation measure could not differentiate between niche and neutral metacommunities if demographic stochasticity were present. The abundance-based β -null deviation measure was successful in distinguishing between niche and neutral metacommunities and was robust to the presence of stochasticity, changes through time, and changing assembly mechanisms. However, we suggest that it is not robust to changing abundance evenness distributions or sampling of communities, and so its interpretation still requires some care. We encourage the testing of the assumptions behind null models for ecology and care in their application.

There are two traditionally separate approaches to understanding ecological community structure. Theoretical approaches rely on mathematical models of species interactions to predict the resulting dynamics, including species coexistence, community diversity, stability, and evenness. Alternately, empirical approaches (both experimental and observational) rely on sampling existing or constructed ecological communities and collecting data on species' identities or abundances, and then analyzing observed presence/absence or abundance patterns using statistical models. Merging theoretical and empirical approaches is often problematic, as it is difficult to connect observed patterns with models of community processes: a single mechanism may produce multiple patterns depending on parameter values, while multiple mechanisms may lead to convergent patterns (Mackey and Currie 2001, Mayfield and Levine 2010).

Null models, which compare observed statistical patterns to those expected in the absence of a particular assembly mechanism (Colwell and Winkler 1984, Gotelli and Graves 1996, Ulrich and Gotelli 2007), represent one common approach for connecting statistical patterns to assembly mechanisms. Null models randomly sample ecological data

to generate patterns representative of random or 'null' processes; empirical data are then compared to the generated null distribution and differences from null are often used to infer the specific processes, which are (or are not) structuring the community. Null models in a variety of formulations have been used to explore community co-occurrence patterns (Connor and Simberloff 1979), community phylogenetic patterns (Kembel 2009), assembly rules (Weiher and Keddy 1999), and macroecology (Colwell and Winkler 1984) and are a fundamental component of modern ecological analysis.

Local and regional diversity, and the ecological processes creating observed diversity patterns, are often the focus of empirical studies: such studies may consider the multiple components of diversity, including local species richness or α -diversity; compositional variance between communities or β -diversity; and regional richness or γ -diversity. α -, β - and γ -diversity are interrelated (Jost 2007), and thus when local richness is low, small changes in composition can have disproportionate effects on β -diversity, making it difficult to differentiate meaningful (process-driven) changes in β -diversity from those resulting from random variability in

species identity and low local richness. To control for this, Chase and colleagues (2011) emphasized the use of β -null deviation: a null model to account for such changes in β -diversity while controlling for stochastic variation and associated changes in α -diversity (i.e. local species richness) (see also Crist et al. 2003). β -null deviation methods have also been used to correct for the interrelation between α -diversity and β -diversity (Grman and Brudvig 2014). It logically follows that if observed communities are more or less similar than expected compared to null communities, this could provide evidence for certain community assembly mechanisms and, therefore, that β -null deviation values could also be used as indices of community structure (Chase 2010).

The β -null deviation method as introduced in Chase et al. (2011) relies on occurrence (presence/absence) data and uses a null model to generate a distribution of β -diversity values expected when artificial communities, equal in α -diversity to the observed communities, are randomly assembled from the regional species pool. The observed β -diversity is then compared to this null distribution, e.g. $\beta_{obs} - E(\beta_{null})$, where $E(\beta_{null})$ is the expected value of the β_{null} distribution. The resulting value represents β -diversity that is independent of α -diversity. As such, null deviation values may represent communities that are more similar than expected by chance (a negative null deviation value), less similar than expected by chance (a positive null deviation value), or close to the chance expectation (values near zero). Large deviations from the random expectation have been interpreted as reflecting communities structured by non-neutral assembly mechanisms, such as shared environmental filtering (negative values; communities more similar than expected by chance) or competitive interactions (positive values; communities less similar than expected by chance) (Chase 2010, Chase and Myers 2011). Of course, other processes (or combinations of processes) may produce negative or positive β -null deviation values but these interpretations of β -null deviation measure dominate applications of the measure.

Additional formulations of β -null deviation incorporate local densities to more finely understand how community structure might diverge from random expectations: the null model in such approaches removes spatial aggregation within and among species and possible effects of random sampling (Kraft et al. 2011, Stegen et al. 2013). In these, the random communities are constructed by shuffling individuals of each species among sites, while maintaining each species' total abundance in the metacommunity. Abundance-based measures may be more robust to minor variation in community composition, such as occurs when a species' local population is maintained by dispersal from source populations.

The usage of β -null deviation measures in this capacity – to hint at underlying assembly mechanisms – has increased rapidly across multiple sub-disciplines (Azeria et al. 2011, Siepielski and McPeck 2012, Stegen et al. 2012, Ferrenberg et al. 2013, Germain et al. 2013, Guo et al. 2013, Rocha-Ortega and Favila 2013, Tanentzap et al. 2013, Püttker et al. 2014, Segre et al. 2014, Mori et al. 2015). Most papers citing the Chase et al. (2011) methods paper include the term “assembly” in the title or abstract, reflecting the trend for the increasing usage of β -null deviation as an index of assembly processes, rather than simply as a null model for β -diversity that controls for differences in α -diversity. Despite the

growing popularity of this approach to disentangle ecological processes in observational data, there are a number of issues that currently remain unaddressed. First, the papers that originated the method and those that have applied it are inconsistent in their interpretation of the β -null deviation values. While deviation from zero is consistently interpreted as reflecting some ecological structuring process, exactly what process drives changes in the value of the β -null deviation is unknown and interpreted in multiple ways. Initial usage (Chase 2010, Chase et al. 2011) suggested that deviations from zero in β -null deviation values might reflect deterministic assembly. Values near to zero were interpreted as showing increasingly stochastic assembly of communities (since stochasticity in assembly should result in greater randomness in community composition, implying that such communities would appear similar to those assembled by randomizing the empirical data) while values much greater or much less than zero were suggestive of deterministic processes driving community assembly. More recently the measure has been interpreted as differentiating between niche versus neutral processes (Ferrenberg et al. 2013, Püttker et al. 2014). Values closer to zero were interpreted as neutral communities, where species are ecologically equivalent to one another. Deviations from zero were interpreted as niche structured communities, where increasing ecological differences among species in heterogeneous environments cause greater deviations from zero. Other interpretations suggest that β -null deviations could capture dispersal limitation or homogenizing dispersal versus drift (Stegen et al. 2012). Which, if any, of these interpretations best reflects the meaning of the β -null deviation measure is unexplored.

One outcome of the popularity of this measure for empirical studies is that mechanistic interpretations have not kept pace – for example, null deviation values of zero have been interpreted as representing both ‘stochastic’ and ‘neutral’ assembly; differences from zero have been interpreted as representing both ‘niche’ and ‘deterministic’. These terms are not interchangeable (Leibold and McPeck 2006, Vellend et al. 2014), and clarifying the precise interpretation of β -null deviation values would greatly benefit our understanding of processes in natural systems. Demographic rates such as birth, death, and dispersal are key. An interpretation of ‘neutrality’ reflects that species are ecologically equivalent and so share identical demographic rates (Hubbell 2001), while ‘stochasticity’ implies that there is random variation in demographic rates (i.e. they are probabilistic) without implying anything about the mean values of those demographic rates (Table 1). Similarly, ‘niche’ processes imply differentiation in mean demographic rates between species (Carroll et al. 2011), while ‘determinism’ indicates an absence of random variation in species’ demographic rates. Though simplistic, one can interpret the niche-neutral axis as reflecting differences in mean demographic rates or lack of differences, while the stochastic-deterministic axis reflects the presence or absence of probabilistic variation about those mean demographic rates. Vellend et al. (2014) reduce these two axes/dimensions to a single dimension with a continuum from drift (neutral stochasticity) to selection, but our categorization is useful for exploring the full range of models and contains their broader conceptualization as a special case. For example, a system may be both neutral (mean

Table 1. Definition of the focal four processes affecting community assembly – as modelled in this study – including details on how they are incorporated into the model described in Eq. 1.

| Term | Definition | Model | Term |
|---------------|--|--|---|
| Niche | Ecological differentiation between species in a community | Each species has an optimal patch where its growth rate is maximum, with lower growth in the sub-optimal patches | $R_{optimal} > R_{sub-optimal}$ |
| Neutral | Ecological equivalence of species in a community | All species have identical growth rates to one another in all patches | $R_{optimal} = R_{sub-optimal}$ |
| Deterministic | Processes are non-probabilistic, invariant outcomes of the system's inputs | Growth and dispersal rates are fixed | R_{ix} is fixed according to values in Table 2 and $m = 0.05$ |
| Stochastic | Processes are probabilistic and affected by randomness, such as through demographic variability in birth, death, and dispersal rates | Growth and dispersal rates are drawn from distributions (Poisson and binomial, respectively), where the mean is equivalent to the deterministic rate | $R_{ix} N_{t,ix} \sim Pois(\mu_{ix} N_{t,ix})$ $\mu_{ix} = R_{ix} \frac{1}{1 + \alpha \sum_j N_{t,jx}}$ $m_{ix} R_{ix} N_{t,ix} \sim Bin(R_{ix} N_{t,ix}, m)$ |

demographic rates constant across species) and deterministic (no variation about these demographic rates), and as a result dynamics in such a system would differ from those expected from a neutral and stochastic (variation about demographic rates) system (Adler et al. 2007). Natural communities of course are unlikely to exist at the extremes of these two axes, and instead will be structured by multiple levels of these processes, e.g. demographic stochasticity and niche differentiation (Adler et al. 2007, Vellend et al. 2014). In the case of multiple structuring processes, the interpretation of β -null deviation values is altogether unexplored.

The meaning of β -null deviation values cannot be determined using observational data alone, but rather requires that the β -null deviation measure be applied to communities assembling with known processes (whether neutral, niche, deterministic or stochastic). This will help clarify the interpretation of the null deviation measure and its robustness to differences in assembly processes and in communities with multiple processes at play. Like a statistical null hypothesis (H_0), the null model for β -null deviation values may find, for a given community, that data differ from a random distribution of species. Without testing against simulated communities with known assembly processes, we cannot infer which particular ecological process may create this significant difference, as the β -null deviation measure is currently used to do. The connection between a statistical null model and the ecological 'null' process it is supposed to represent must be justified. The null model at the heart of the β -null deviation measure could differ substantially in community structure from a neutral community model – the mechanistic ecological 'null' model. Appropriate tests of the β -null deviation measure for communities with known assembly processes (whether neutral, niche, deterministic or stochastic) are lacking, and its robustness to changes in ecological parameters and assembly processes remains unknown.

In this paper, we use simulated metacommunities to explore how both stochastic and deterministic formulations of metacommunity models with varying strengths of niche structure alter the value (and interpretation) of the presence/absence and abundance β -null deviation measures, and thus the

appropriate use of the measure for inferring assembly mechanisms. We show that β -null deviation values near zero occur when assembly dynamics are neutral, and the absolute value of the measure diverges from zero when assembly dynamics are niche-based. However, this is only true in specific cases. We show that 1) stochasticity, 2) changes in assembly mechanism thru time, and 3) population drift through time alter the value of the presence/absence β -null deviation in unexpected ways, but that the abundance β -null deviation measure is robust to these processes. Finally, we provide a discussion of the conditions for which null deviation measures may be appropriate for inferring community assembly processes.

Methods

We generated replicated artificial data using a metacommunity model: β -diversity and β -null deviation values were then calculated using these data. Further, we varied parameters of the model to generate metacommunities along a gradient from niche to neutral structure. We also generated both deterministic and stochastic versions of metacommunities.

Mathematical formulation of metacommunity model

We created a discrete time mechanistic metacommunity model of 25 species and 25 patches (e.g. a habitat patch that can contain a local community). The model includes birth and death of individuals, inter- and intra-specific competition for space within patches, and migration between patches. The model with global migration between patches is a patch model and not spatially explicit (Mouquet and Loreau 2003) (although it could be made spatially explicit). Dynamics within patches were modeled using the classic competition form of the Beverton–Holt model (Beverton and Holt 1957, Leslie and Gower 1960):

$$N_{t+h,ix} = R_{ix} N_{t,ix} \frac{1}{1 + \alpha \sum_j N_{t,jx}} \quad (1)$$

where N represents the population of a given species i in patch x at time t , and $t + h$ is the time up until just before migration. R_{ix} is the density-independent growth rate of species i in patch x , which depends on the niche-structure in the simulation (see Table 2 for parameter values). The term $1 + \alpha \sum_j N_{t,jx}$ is the competition experienced by species i (Chesson 2000), where α is the competition coefficient ($\alpha = 1/600$ for all simulations). Migration occurred after within-patch dynamics. For global dispersal, metacommunity dynamics were given by

$$N_{t+1,ix} = N_{t+h,ix} + m \left(\sum_{z \neq x} \frac{N_{t+h,iz}}{p-1} - N_{t+h,ix} \right) \quad (2)$$

where m is the migration rate, z indexes patches, and p is the total number of patches (25 for all analyses). To model local dispersal, we modified the above global dispersal model (Eq. 2) into a coupled map lattice (Brännström and Sumpter 2005). For local dispersal, an individual could only migrate to a patch directly adjacent in one of the four cardinal directions (5×5 lattice). We present results from global and local dispersal with $m = 0.05$. Lower values of m did not lead to results qualitatively different from those presented here; higher values of m produced metacommunities with β -null deviation values closer to zero (Supplementary material Appendix 1 Fig. A1). We started all simulations with 150 individuals of each species in each patch.

Because the deterministic model has abundance on a continuous scale (i.e. there can be less than one individual), by definition no species ever goes extinct in a patch. For deterministic models, we therefore applied a detection threshold of two individuals per species to determine presence/absence – this is a conservative choice representing the minimum requirement for reproduction in a sexual population.

Stochastic and deterministic versions of the model

The above deterministic model is the mean field counterpart to its stochastic version (Hiebeler 1997), in which we include demographic stochasticity for births and dispersal (Table 1). We incorporated demographic stochasticity by drawing the

Table 2. Species' density-independent growth rates for their optimal (niche) and sub-optimal patches in the metacommunity, for each of the five metacommunity types. Parameter values are listed for cases with regional neutrality, and without regional neutrality.

| | Regional neutrality | Community type | Growth rate, optimal patch (R_{optimal}) | Growth rate, sub-optimal patch ($R_{\text{sub-optimal}}$) |
|-----------------------|---------------------|----------------|---|---|
| Niche ↓ Neutral | yes | 1 | 1.45 | 1.095833 |
| | yes | 2 | 1.35 | 1.1 |
| | yes | 3 | 1.25 | 1.104167 |
| | yes | 4 | 1.15 | 1.108333 |
| | yes | 5 | 1.11 | 1.11 |
| Niche ↓ Neutral | no | 1 | unif(1.55, 2.1) | unif(1.0, 1.22) |
| | no | 2 | unif(1.45, 1.9) | unif(1.0, 1.22) |
| | no | 3 | unif(1.35, 1.7) | unif(1.0, 1.22) |
| | no | 4 | unif(1.25, 1.4) | unif(1.0, 1.22) |
| | no | 5 | 1.11 | 1.11 |

number of individuals at a given time from a Poisson distribution, where the mean of the distribution equaled N_{t+h}/N_t from Eq. 1. This allows for stochasticity in both births and survival (Melbourne and Hastings 2008). Stochasticity in dispersal followed a binomial distribution (Table 1) where individuals dispersed with equal probability to all non-focal patches. Supplementary Appendix 2 contains R code for model simulations and analyses.

Establishing metacommunities along a niche to neutral gradient

To create a gradient from niche to neutral, we varied density-independent growth rates, R_{ix} , among patches between the five scenarios (Table 2 shows parameter values). Differences in R_{ix} can be interpreted as representing differences in the species' responses to the abiotic environments of the patches. The metacommunity with the greatest niche structure (type 1 in Fig. 1) had the largest difference in growth rate between the optimal patch (e.g. niche) for each species compared to all other patches. In this scenario, competitive exclusion of all species not in their optimal patches occurred, creating a species-sorting metacommunity (Leibold et al. 2004). At the other extreme, the metacommunity was neutral, where all species had identical density-independent growth rates in all patches (type 5 in Fig. 1). Metacommunities of types 2, 3 and 4 were intermediate between species sorting and neutrality. For all metacommunity types, we held average fitness equal among all species at the metacommunity level, thus removing any effect of variation in average fitness among metacommunities and among scenarios. Thus, although species had niches or different growth rates in patches within the metacommunity, their average fitness across the metacom-

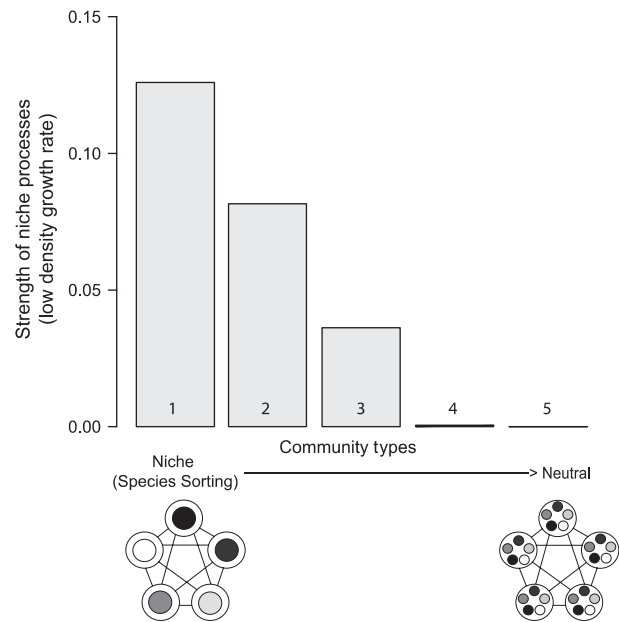


Figure 1. Strength of niche processes as measured by the magnitude of stabilizing coexistence mechanisms for the five possible models of metacommunity assembly, ranging from niche-structured (type 1, species sorting), to neutral (type 5) in which species co-occur in all patches. Model parameter values are listed in the Methods and Table 2.

munity was identical (“regional similarity”, Mouquet et al. 2003). This assumption of regional similarity controls for the effect of fitness difference variation on the β -null deviation measure, allowing us to explore the effects of changes in local structuring processes while controlling for regional level contributions to local coexistence.

Quantifying the strength of stabilizing coexistence mechanisms

We quantified the relative strength of niche-partitioning within each community type using the spatial coexistence mechanisms defined by Chesson (2000). We measured the strength of stable coexistence as the tendency of a focal species to recover from low density (the long term low-density growth rate) while the rest of the community was at equilibrium for deterministic models or stationarity for stochastic models (Armstrong and McGehee 1980, Turelli 1981, Chesson 2000). Because the average, metacommunity level fitness was equal for all species, low-density growth rate reflected contributions to coexistence exclusively from two stable coexistence mechanisms: fitness-density covariance and the spatial storage effect, which together define the spatial niche of a species (Chesson 2000, Valladares et al. 2008). Thus, the magnitude of the low-density growth rate is the sum of the contribution of these stabilizing mechanisms along the gradient from niche separation (species-sorting) to neutrality. In the neutral case, the low-density growth rate is zero, indicating a lack of stabilizing mechanisms and a metacommunity structured exclusively by equalizing mechanisms (Adler et al. 2007).

Removing regional similarity of species

To explore whether the absence of regional similarity alters our findings, we also constructed stochastic metacommunities in which species do not exhibit metacommunity-level neutrality. Following Melbourne et al. (2007), we did this by randomly drawing growth rates for each species in each patch from uniform distributions (Table 2). If that species coexisted with all other species thus far drawn (i.e. had a positive low-density growth rate), we kept that species for the simulation. If the species was unable to coexist, it was removed. We repeated this process until a metacommunity with 25 coexisting species was obtained: we used this process to produce 50 replicates of each metacommunity type.

β -null deviation calculation

β -null deviation values indicate the magnitude of deviation between the observed β -diversity (β_{obs}) and the expectation for β -diversity, $E(\beta_{\text{null}})$, from a randomly assembled pair of patches. We follow the method described in Chase et al. (2011) for the presence/absence β -null deviation measure. β_{obs} represents the pairwise Jaccard dissimilarity between two patches. To determine the null expectation $E(\beta_{\text{null}})$ for this pair of patches, 1000 pairs of patches – with α -diversity matched to the observed two patches – were then assembled by randomly selecting species weighted by their observed frequency in the metacommunity. Pairwise β -diversity between the 1000 randomly assembled pairs of patches was then cal-

culated to produce a distribution of null β -diversity values: the null deviation value represents the difference between the observed pairwise β -diversity and the mean of the null distribution of β -diversity values (that is, $\beta_{\text{obs}} - E(\beta_{\text{null}})$). For a metacommunity, the overall β -null deviation was the mean deviation across all patch pairs.

Abundance-based β -null deviation values used the same procedure but with a different dissimilarity metric and null model. We used the Bray–Curtis dissimilarity metric, which takes account of species’ relative abundances (Tuomisto 2010). The null model was created by randomly placing each observed individual into a patch until every individual had been placed into a patch in the metacommunity (Kraft et al. 2011, Stegen et al. 2013). This maintains the observed metacommunity-level abundance distribution but randomizes the location of individuals. See Supplementary Appendix 2 for R code for all β -null deviation calculations.

Analyses

We calculated both presence/absence and abundance-based β -null deviation measures for four distinct scenarios. In scenario 1, we examined how β -null deviation values changed for metacommunities along the gradient from niche to neutral assembly (types 1–5), for both deterministic and stochastic formulations of the model. We allowed dynamics to continue for 150 generations to ensure that analyses captured the equilibrium state (deterministic) or stationary distribution (stochastic) rather than transient dynamics, and then calculated β -null deviation measures. In scenario 2, we explored how the β -null deviation measure captures transient dynamics in stochastic models for niche (type 1) and neutral (type 5) communities. We measured β -null deviation for 750 generations (measuring values at 10, 50, 100, 150, 250, 500, 750 generations) while holding all parameters constant. In scenario 3 we considered the effect of changes in assembly mechanism through time, such as is typical in manipulative experiments. After the metacommunity reached its equilibrium (deterministic) or stationary distribution (stochastic), we applied a simulated experimental treatment that caused either 1) a niche structured metacommunity to become neutrally structured (parameter values changed from type 1 to type 5) or 2) a neutral metacommunity to become niche structured (parameter values change from type 5 to type 1). We then compared the β -null deviation values before treatment to a 150-generation time-series after the treatment for both stochastic and deterministic versions of the model. In scenario 4, we examined how β -null deviation values changed along a gradient from niche to neutral assembly (types 1 through 5), but this time removing the constraint of regional similarity. In all analyses of stochastic models, we simulated 50 metacommunities for each model type and calculated the β -null deviation measure for each metacommunity.

Effect of degree of regional species pool sampling on β -null deviation

Thus far we have assumed a complete census of the regional species pool. However, observational data are typically from a sample and involve uncertainty about the true abundances of

species in a region. To examine the effect of this uncertainty, we sampled less than the true number of patches in the 25 species metacommunity, including only 5, 10, 15 or 20 local patches from the 25-patch metacommunity to calculate the null deviation measure. We repeated the sampling 250 times for each level to determine whether the accuracy of the abundance-based measure varied with the proportion of sites sampled from the metacommunity. Results for samples of 10, 15 and 20 patches fell predictably between those of 5 patches and all 25 patches, so we present results from the most extreme case (only 5 patches or 20% of the metacommunity).

Results

Niche to neutral gradient

We confirmed that the species-sorting (type 1) to neutral (type 5) metacommunity gradient represented a gradient of niche strength. Along the niche to neutral gradient, metacommunities of type 1 (species-sorting) had the highest low-density growth rate (Fig. 1), which declined in each metacommunity type to a value of 0 for neutral communities. This means that in neutral metacommunities, while species did not drive others towards extinction, they did not have a tendency to recover from low-density. Thus, stabilizing coexistence mechanisms (or niches) were strongest in type 1 metacommunities and absent from type 5 metacommunities, which were structured exclusively by equalizing mechanisms.

Scenario 1

Jaccard dissimilarity β -diversity values for the deterministic metacommunities varied from 1 (patches differ completely in their composition) to 0 (patches have identical compositions), respectively, along the gradient from niche-structured to neutral metacommunities. Values of the presence/absence β -null deviation measure reflected the changing structure along this gradient. They distinguished between neutral or near-neutral metacommunities (types 4–5), which had β -null deviation values of zero – indicating an absence of niche processes – and niche metacommunities (1–3), which had values larger than zero (Fig. 2a; Supplementary material Appendix 1 Table A1) – indicating niche processes were causing patches in a metacommunity to be more dissimilar than expected. The abundance β -null deviation measure also varied for metacommunities along this gradient: from mean values of 0.793 for niche structured metacommunities (type 1) to -0.341 for neutral metacommunities (type 2). Negative β -null deviation values suggest that species composition is more similar between patches than expected under the null model of random assembly. This makes sense because, in contrast to the null model, deterministic neutral communities are not randomly assembled thus removing a source of dissimilarity. The abrupt jump in β -null deviation values between metacommunities of type 3 and 4 in the deterministic case reflects the detection threshold.

We considered the same gradient of assembly for stochastic metacommunity models. Compared to deterministic metacommunities, which had little variability in

β -null deviation values, stochastic metacommunities had more variability in β -null deviation values, indicated by the greater interquartile range (Fig. 2b; Supplementary material Appendix 1 Table A1). Variability in β -null deviation in deterministic metacommunities is due exclusively to Monte Carlo error induced by the null model, whereas variability in β -null deviation in stochastic models reflects variability in metacommunity structure. Monte Carlo error is the error in the null deviation that arises because its estimate relies on a stochastic simulation of the null model (Hammersley and Handscomb 1964, Koehler et al. 2009). Mean β -diversity values ranged between approximately 0.5 and 0.7, indicating patch level composition, on average, was quite dissimilar. The presence/absence β -null deviation values ranged between $0.016 (\pm 0.190)$ to $-0.05 (\pm 0.062)$ for niche and neutral metacommunities (here and elsewhere, we report mean \pm SD). The trend toward more negative values of β -null deviation for neutral metacommunities suggests that species composition of patches in the metacommunity is more similar than expected under the null model of random assembly. This shows that the null model does not correctly capture beta diversity for the neutral metacommunities. β -null deviation values for the abundance version of the measure varied between $0.739 (\pm 0.018)$ to $0.367 (\pm 0.064)$ for niche through neutral metacommunities, declining consistently toward zero along the niche-neutral gradient. Positive values of the β -null deviation measure for neutral metacommunities suggest that species composition was less similar between patches compared to the random expectation.

Deterministic and stochastic model results did not depend on dispersal type, suggesting they are robust to variation in dispersal strategies, ranging from restricted local movement to global dispersal (Supplementary material Appendix 1 Fig. A2).

Scenario 2

For stochastic niche structured metacommunities, the presence/absence β -null deviation measure did not vary greatly over 750 generations (measured at generations 10, 50, 100, 150, 250, 500 and 750 generations), $\mu \pm \sigma$: -0.001 ± 0.011 , 0.003 ± 0.016 , 0.002 ± 0.016 , 0.001 ± 0.017 , 0.002 ± 0.015 , 0.002 ± 0.015 , 0.002 ± 0.016 . All values were close to zero, the expectation for neutral rather than niche metacommunities. Values for abundance β -null deviations initially rose, in response to the non-equilibrium starting conditions, and then remained constant with positive values over the 750 generations (measured at generations 10, 50, 100, 150, 250, 500 and 750 generations): 0.350 ± 0.039 , 0.750 ± 0.015 , 0.750 ± 0.015 , 0.750 ± 0.016 , 0.750 ± 0.016 , 0.750 ± 0.015 , 0.750 ± 0.015 (Fig. 3).

For stochastic neutral metacommunities, presence/absence β -null deviation values initially centered at zero (as expected), but became more negative with time and increased in variance (for time points 10–750: -0.001 ± 0.010 , -0.016 ± 0.034 , -0.040 ± 0.044 , -0.057 ± 0.052 , -0.066 ± 0.057 , -0.082 ± 0.070 , -0.084 ± 0.072). The abundance-based β -null deviation values for stochastic neutrally structured metacommunities rose slightly and then

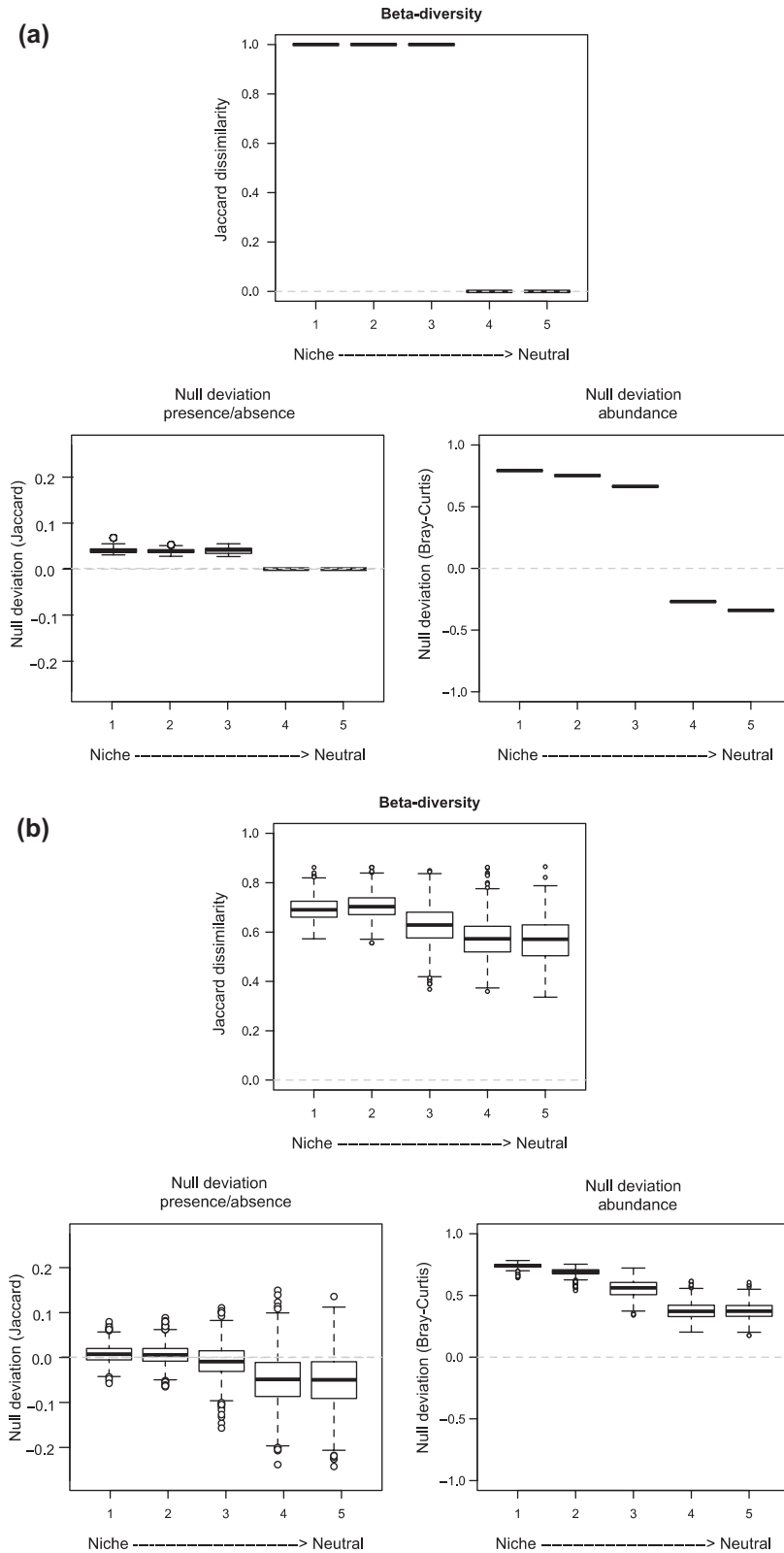


Figure 2. β -null deviation values from simulated metacommunity models, for five assembly types representing a gradient from niche to neutral. Subplots show β -diversity (Jaccard), presence/absence β -null deviation values, and abundance β -null deviation values for (a) deterministic metacommunity models and (b) stochastic metacommunity models. Each bar represents 50 replicate metacommunities (see Methods): dark lines show the mean value, whiskers capture the interquartile range, and points show extreme values. Note that y-axes differ for presence/absence and abundance β -null deviation results.

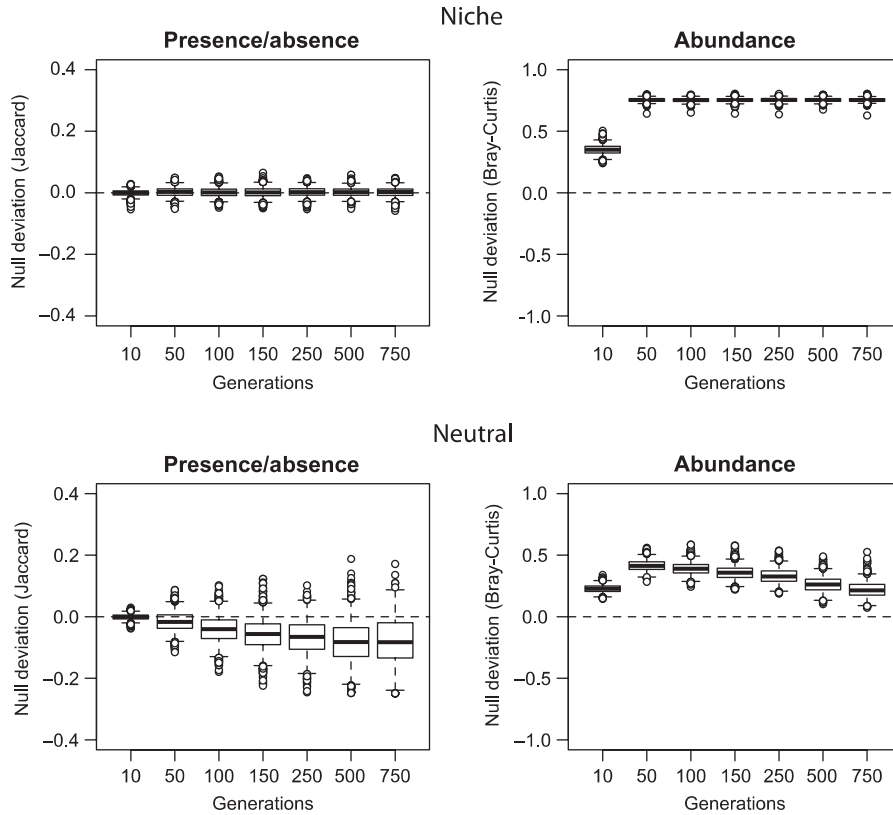


Figure 3. Changes in β -null deviation values over time. β -null deviation results are shown for niche-structured metacommunities (type 1) and neutrally-structured metacommunities (type 5) for stochastic models, where dynamics were allowed to continue for 750 generations. Both presence/absence and abundance β -null deviation measures were calculated. Each bar represents 50 replicate metacommunities. Note the x-axis is categorical, not a continuous scale.

declined through time, although values remained positive (for time points 10–750: 0.228 ± 0.032 , 0.415 ± 0.044 , 0.391 ± 0.044 , 0.359 ± 0.051 , 0.332 ± 0.057 , 0.265 ± 0.061 , 0.222 ± 0.066).

Scenario 3

In both scenarios (a change from niche to neutral assembly, and a change from neutral to niche assembly), although the value of the presence/absence measure changed, it did not change in the way expected to correctly detect the structuring mechanism (i.e. the experimental treatment) (Fig. 4). In the niche to neutral scenario presence/absence β -null deviation values became increasingly negative, falsely indicating an increase in community structure compared to randomly assembled communities: at the start of the experiment, the mean β -null deviation value was $0.007 (\pm 0.020)$ and after 150 generations it was $-0.052 (\pm 0.061)$. Variance in β -null deviation also increased over time. Conversely, in the neutral to niche scenario, presence/absence β -null deviation values were initially negative (-0.045 ± 0.058) but after the simulated experimental treatment, the β -null deviation values increased to near zero (-0.001 ± 0.02), falsely suggesting a neutral metacommunity rather than a niche-structured metacommunity.

The abundance based β -null deviation measure performed better, declining towards zero after a change to neutral assembly (from 0.740 ± 0.067 at $t = 0$ to 0.377 ± 0.067 at $t = 150$), and becoming increasingly positive after a change to niche assem-

bly processes (from 0.383 ± 0.125 at $t = 0$ to 0.587 ± 0.125 at $t = 150$). Variance in β -null deviation between realizations in the stochastic neutral to niche models was largely a result of variation in the state of neutral metacommunities (resulting from stochasticity) just before the switch to niche processes.

Scenario 4

Removing the regional similarity constraint did not alter the distribution of β -null deviation values along the niche-neutral gradient (Fig. 5). Results were qualitatively similar to those from the stochastic metacommunity with regional similarity (Fig. 2b).

Effect of degree of regional species pool sampling on β -null deviation estimates

Sampling the metacommunity resulted in higher null deviation values than those from a complete census of the metacommunity (Fig. 6). There was a significant interaction between sample size and metacommunity type: niche metacommunity β -null deviation values were more biased when under-sampled while neutral metacommunities were more uncertain.

Discussion

The β -null deviation measure, initially developed as a null model for β -diversity, has increasingly been used as an

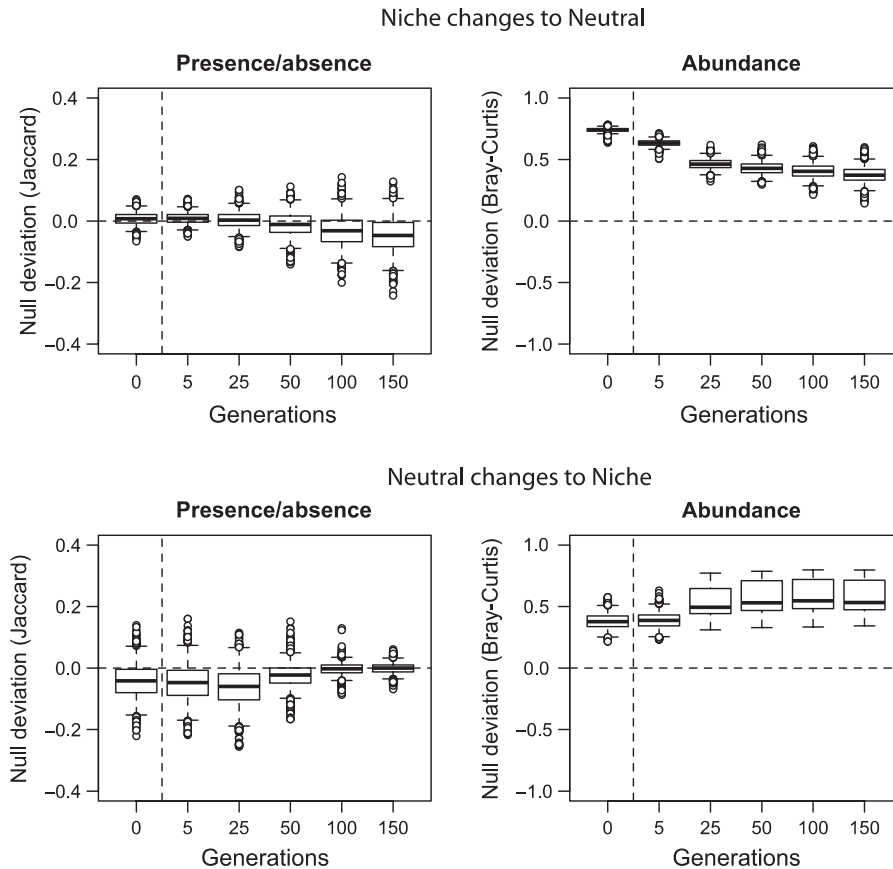


Figure 4. The effect of changes in assembly processes on β -null deviation values. Figure shows the effect of changes from niche to neutral assembly (top) and from neutral to niche assembly (bottom) over time, for stochastic metacommunity models. Both presence/absence and abundance β -null deviation measures were calculated. Each bar represents 50 replicate metacommunities. Note the x-axis is categorical, not a continuous scale.

index of community assembly mechanisms and applied to empirical data. This analysis compared β -null deviation for simulated communities with known assembly mechanisms to determine how values of the β -null deviation measure should be interpreted and how effectively it performs in this role. Our results help to clarify the correct interpretation of the β -null deviation measure: we found that its values differentiate between niche (values further from zero) and neutrally structured metacommunities (values nearer to zero). This is in contrast to the interpretation of deterministic versus stochastic processes (Chase and Myers 2011, Stegen et al. 2013). The presence/absence β -null deviation measure was not robust to the effect of demographic stochasticity on assembly, so we cannot recommend it. In contrast, the abundance based measure changed consistently along the niche-neutral gradient and to changes in assembly, although its utility is primarily as a comparative (focusing on changes in value), rather than absolute measure.

How should β -null deviation values be interpreted?

In the absence of any stochasticity, presence absence β -null deviation values relate – as originally assumed – to the structuring processes assembling a community. Values of zero differentiate neutral communities from those that are niche structured (absolute values much greater than zero). This differs from the original interpretation of β -null deviation

values (Chase 2010, Chase et al. 2011), which suggested that values near zero reflect stochastic assembly processes and those different from zero reflect deterministic processes. Instead, we show that, for the presence/absence measure, the null expectation for β -diversity between random samples of species from the regional species pool converges on the expectation for a neutral community, i.e. all species are similarly likely to be present in a patch. Thus the statistical null model reflects our neutral model of assembly.

Performance of different versions of the β -null deviation measure

We found that β -null deviation measures varied in their properties depending on whether they were calculated using presence/absence or abundance data. In particular, the presence/absence measure was not robust to 1) stochasticity in assembly, 2) the number of generations from assembly to sampling (due to variation from stochasticity in population dynamics), and 3) changes in assembly mechanisms through time. Demographic stochasticity in particular affects the β -null deviation measure, because it decreases the relative differences in β -null deviation between niche and neutral communities while increasing variance, making it difficult to correctly distinguish between these mechanisms. This difficulty is enhanced when assembly mechanisms change through time. For example, historical contingency can alter

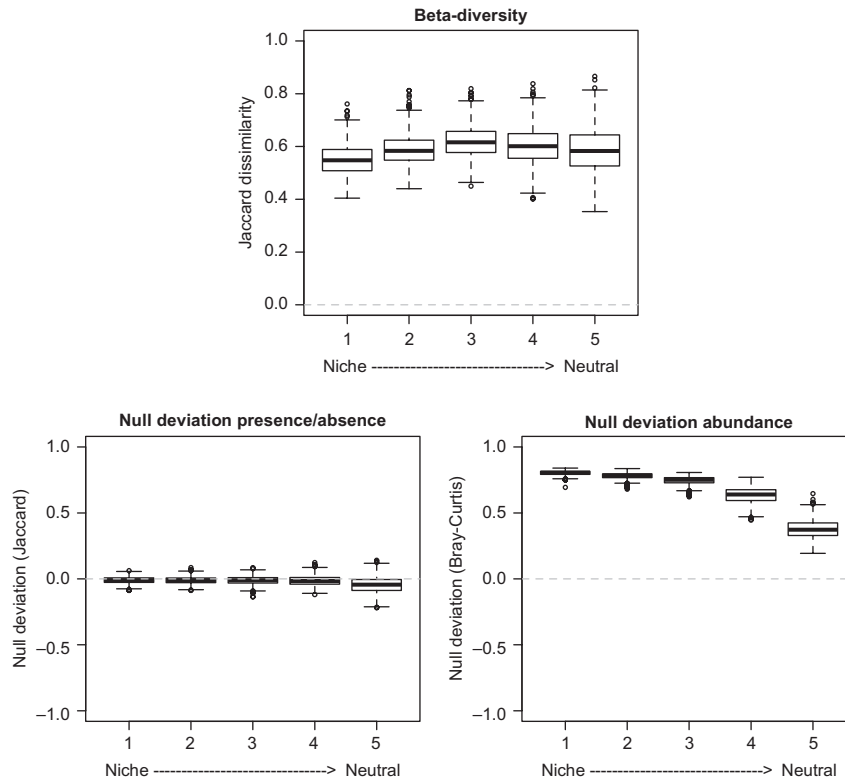


Figure 5. β -null deviation values from simulations of stochastic metacommunities when species do not have equal fitness at the metacommunity scale (i.e. in the absence of regional similarity). See Methods for the five assembly types.

community structure far from the expectation for niche or neutral assembly, and the presence/absence measure is not robust to such contingency. The presence/absence β -null deviation measure (and many presence/absence based null models) relies on variation in species identity between local communities to distinguish between structuring processes:

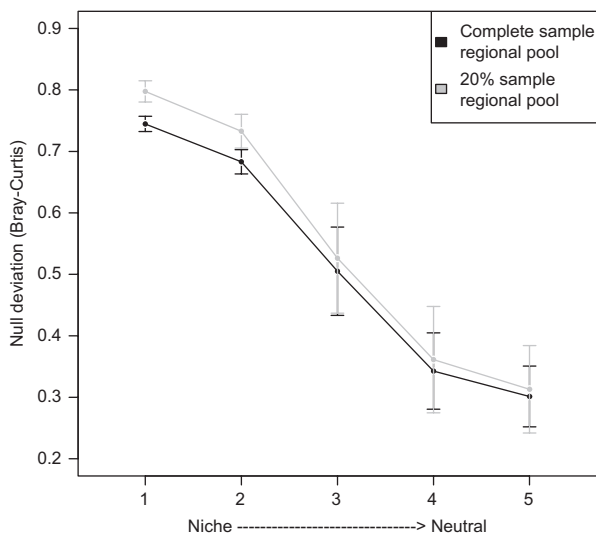


Figure 6. Effect of incomplete sampling of the regional species pool for abundance-based null deviation metric values. Error bars represent standard deviations for 50 replicates of the sampling procedure (see Methods).

except in highly diverse metacommunities, there is often not enough variation in species' composition to provide strong evidence for a particular assembly process.

The abundance-weighted β -null deviation measure was developed in part because of such limitations, and is used to control for the effects of spatial aggregation of individuals in samples (Stegen et al. 2012). Performance of this measure was markedly better than that of the presence/absence version: the absolute value of the abundance-weighted β -null deviation measure increased in response to niche processes and declined in response to neutral processes. The abundance-weighted β -null deviation measure was effective in identifying increases or decreases in niche or neutral structure in communities through space and/or time. Further, it behaved reasonably consistently in the presence of stochasticity, through time, and for communities lacking regional similarity, all of which suggests that it is better suited to use with empirical data. However, a number of issues must still be considered. First, similar values of the abundance β -null deviation measure may still reflect different assembly processes, as in Myers et al. (2013), in which the authors showed that β -null deviation values for tropical and temperate forests were similar, but different mechanisms (environmental filtering versus dispersal limitation) produced these similar values. Results of similar magnitudes are not necessarily comparable across different metacommunities: a metacommunity in one system should not be said to be 'more niche structured' because it has a larger β -null deviation value than that measured in a different system. The β -null deviation is not robust to comparisons across systems or habitats, and

likely should be restricted to geographically similar analyses, such as within metacommunities or regions, or across time or experimental treatments for a single locale.

In addition, absolute values of the abundance β -null deviation measure did not correspond with the expectation for niche or neutral communities. The abundance β -null deviation measure reflects changes in aggregations of individuals, but it is also sensitive to changes in abundance evenness distributions. Non-random abundance evenness distributions, such as may result from neutral assembly of patches, can cause null deviation values to diverge from zero, simply because the null model has random (uneven) abundances. This may result in negative values of the β -null deviation metric (e.g. deterministic model, Fig. 2a, where abundances are more even than random), or positive values (e.g. stochastic model, Fig. 2b, where abundances are less even than the random expectation due to stochasticity). The inability to disentangle whether the abundance-weighted β -null deviation measure changes as a result of changing aggregations of individuals, or changing evenness in composition, also limits its utility.

The β -null deviation measure relies on knowing the true abundance distribution of the regional species pool. One important limitation occurs when the true abundance distribution of a regional species pool is unknown, such as due to undersampling of sites or difficulties in delimiting the 'regional pool'. We found that where only 20% of the true metacommunity patches were sampled (e.g. five patches), the decline in the β -null deviation values across the niche-neutral gradient was significantly different from that of the complete sample, though the realized effect size was small (~7%). Because species sorting in our niche-structured metacommunities implies that each patch should have unique species abundances, values of the measure are biased for niche structured metacommunities when there is under sampling of patches in the region. Alternately, a scheme that subsamples individuals in each patch, such as through use of transects or point counts, would tend to be less accurate for stochastic neutral communities (since at each patch many species co-occur and so site abundances are lower if carrying capacity is constant, and under-sampling would increase variation). The issue of accuracy in sampling and defining the abundance-weighted regional species pool is an important one for observational data, where uncertainty is expected. β -diversity measures are sensitive to undersampling (particularly those based on presence-absence data, Beck et al. 2013); compounding this, the reliance of the null deviation measure on the observed abundance or range size distribution provides an additional source of bias when species' abundances or presences are not well reflected by the data. Future work should consider the implications of under-sampling for null models such as this one.

We considered five different strengths of stabilizing coexistence mechanisms, from strong niche differences between species to neutrality, covering three of the four metacommunity paradigms: species sorting, neutrality, and mass effects (Supplementary material Appendix 1 Fig. A1). Our model produced strong gradients in beta-diversity (values from 0–1) as a result of differences in species' innate growth rates in patches, making it a valuable first approach to testing the β -null deviation measure. However, these are likely not the only factors influencing β -diversity in natural systems. Other

drivers of β -diversity, such as speciation, dispersal barriers or limitations, and extinctions, as well as more realistic assumptions (such as larger species pools) should be considered as well. While spatial aggregation may additionally influence the ability of the β -null deviation measure to detect underlying community assembly processes, lowering dispersal rate or using limited local dispersal did not alter our conclusions. However, in well-mixed communities (e.g. a dispersal rate of 50%), increased dispersal causes communities to appear increasingly similar and so measures of β -diversity and community assembly are no longer meaningful (e.g. Supplementary material Appendix 1 Fig. A1).

Conclusion

Though originally developed as a null model for β -diversity, β -null deviation measures are increasingly used as an indicator of the processes structuring communities. They speak to a fundamental issue in ecology – the need to reconcile empirical data, statistical models, and theoretical explanations. However, as with most measures meant to bridge observational and theoretical analyses, many assumptions are needed. This work clarifies for the first time the appropriate interpretation of the β -null deviation measures: to differentiate between niche and neutral communities, rather than between deterministic and stochastic communities. Our results suggest, however, that presence/absence based β -null deviation measures lack the resolution to differentiate between niche and neutral communities, particularly when stochasticity or changes in assembly through time are present, but that the abundance based β -null deviation measure performs adequately under these conditions. However, null models that precisely and robustly disentangle the different processes structuring communities remain elusive.

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Supplementary material (available online as Appendix oik.02803 at <www.oikosjournal.org/readers/appendix>). Appendix 1–2.