

Using null models to disentangle variation in community dissimilarity from variation in α -diversity

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Abstract. β -diversity represents the compositional variation among communities from site-to-site, linking local (α -diversity) and regional (γ -diversity). Researchers often desire to compare values of β -diversity across localities or experimental treatments, and to use this comparison to infer possible mechanisms of community assembly. However, the majority of metrics used to estimate β -diversity, including most dissimilarity metrics (e.g., Jaccard's and Sørensen's dissimilarity index), can vary simply because of changes in the other two diversity components (α or γ -diversity). Here, we overview the utility of taking a null model approach that allows one to discern whether variation in the measured dissimilarity among communities results more from changes in the underlying structure by which communities vary, or instead simply due to difference in α -diversity among localities or experimental treatments. We illustrate one particular approach, originally developed by Raup and Crick (1979) in the paleontological literature, which creates a re-scaled probability metric ranging from -1 to 1 , indicating whether local communities are more dissimilar (approaching 1), as dissimilar (approaching 0), or less dissimilar (approaching -1), than expected by random chance. The value of this metric provides some indication of the possible underlying mechanisms of community assembly, in particular the degree to which deterministic processes create communities that deviate from those based on stochastic (null) expectations. We demonstrate the utility of this metric when compared to analyses of Jaccard's dissimilarity index with case studies from disparate empirical systems (coral reefs and freshwater ponds) that differ in the degree to which disturbance altered α -diversity, as well as the selectivity by which disturbance acted on members of the community.

Key words: β -diversity null model; community assembly; determinism; species pool; stochasticity.

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INTRODUCTION

Recent interest in the patterns of species diversity and community composition across space has resurrected the concept of β -diversity (e.g., Whittaker 1960, 1972), which quantifies the variation in the composition of species from site-to-site, originally defined as the ratio between

local (α) diversity and regional (γ) diversity ($\beta = \alpha/\gamma$). β -diversity can be a useful metric when trying to understand patterns of species diversity across spatial scales (e.g., Veech et al. 2002, Crist and Veech 2006, Jost 2007, Tuomisto 2010a, b, Anderson et al. 2011), and for example, can allow inference about the relative importance of community assembly processes such as those that are

more deterministic (niche-related) relative to those that are more stochastic (e.g., Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Dornelas et al. 2006, Chase 2007, 2010). Unfortunately, a large number of the metrics and statistical analyses used to estimate β -diversity are confounded, are not always directly comparable, and may not produce conceptually meaningful values (Jost 2007, Jurasinski et al. 2009, Tuomisto 2010a, b, Anderson et al. 2011). For example, one of the biggest problems associated with analyses of β -diversity is that using either a multiplicative ($\gamma = \alpha \times \beta$) or additive ($\gamma = \alpha + \beta$) partition, β -diversity is linked to variation in γ and α by definition, thus making statistical comparisons of β -diversity among sites or regions confounded by coincident variation in α or γ (e.g., Wilson and Shmida 1984, Lande 1996, Koleff et al. 2003, Jost 2007, Tuomisto 2010a, b).

There has been recent debate regarding appropriate ways to create α -independence in the evaluation of β -diversity (e.g., Baselga 2010, Jost 2010, Ricotta 2010, Veech and Crist 2010a, b). Although we do not intend to engage directly in this debate, we emphasize that because all three diversity components (α , β and γ) are interconnected, any two of the three components will be statistically dependent on one another, regardless of the diversity measure (e.g., Ricotta 2010). Thus, if there is a change in some factor that influences the number of species that can coexist in any given site (e.g., local disturbance, productivity, predators), influencing α -diversity, it is unclear whether a change in β -diversity is due to differences in the underlying assembly processes that create β -diversity (e.g., deterministic versus stochastic factors), or instead due to differences that result because the factor of interest changed the level of α -diversity, necessarily causing a concomitant change in β -diversity (e.g., Vellend 2004, Vellend et al. 2007, Chase 2007, 2010, Chase et al. 2009). To illustrate with a simple example, if the average number of species per site (α) decreases via random local extinctions (e.g., ecological drift due to a decrease in habitat size) without a proportional change in regional (γ) diversity (e.g., if the number of localities is very large), a change in β will be detected even though there has been no change in the ecological differences or amount of dispersal among localities.

For an empiricist who wants to compare patterns of β -diversity among sites and infer possible mechanisms, a statistical null modeling approach (sensu Gotelli and Graves 1996) provides a straightforward and versatile way to discern to what degree changes in observed β -diversity are influenced by random changes in α -diversity (e.g., Connor and Simberloff 1978, Raup and Crick 1979, Crist et al. 2003, Vellend 2004, Dornelas et al. 2006, Freestone and Inouye 2006, Chase 2007, 2010, Vellend et al. 2007, Belmaker et al. 2008, Leprieur et al. 2008, Chase et al. 2009, Lepori and Malmquist 2009, Smith et al. 2009). A null modeling approach in this context essentially asks: “what would β -diversity look like with a completely random assembly process, given α and γ -diversity?” With this null-expected distribution in hand, one can then ask: “does the observed β -diversity deviate from the null expectation, and if so, by how much?”

In this article, we focus on an approach that is relevant for studies that use (dis)similarity metrics based on presence-absence data comparisons between two communities (e.g., Jaccard’s or Sørensen’s dissimilarity metrics). These dissimilarity metrics are often used as an estimate of β -diversity (e.g., Vellend 2001, Koleff et al. 2003). We first illustrate how one of the most commonly used metrics to estimate β -diversity, Jaccard’s dissimilarity index, is strongly influenced by the number of species that live in each site (e.g., α -diversity) and the number of species that live in the regional species pool (γ -diversity). As such, a large number of studies that have compared such dissimilarities among communities that vary in α -diversity can not discern whether the differences in dissimilarity actually result from differences in the compositional variation among local communities, or just due to differences among those communities in α -diversity. We next overview one particular null modeling approach that allows the quantification of the degree to which pairwise community dissimilarity differs from that which would be expected by random chance alone. We conclude with a discussion of the utility and limitations of this approach, and point toward a family of related approaches that will allow a more thorough investigation of the mechanisms underlying patterns of community compositional differentiation across sites.

A null expectation for community (dis)similarity when α -diversity varies

First, we illustrate how the value of incidence-based pairwise (dis)similarity indices such as Jaccard's index depend on α -diversity. That is, when comparing among regions (or habitat types, experimental treatments, time periods, etc.), changes in (dis)similarity cannot be disentangled from changes in α -diversity among those regions unless this dependence is explicitly considered (Fig. 1). For two samples with α_1 and α_2 species selected with equal probability from a pool of γ -species, the expected number of shared species (SS_{exp}) is an accelerating function of α -diversity: $SS_{exp} = \alpha_1\alpha_2/\gamma$ (Connor and Simberloff 1978). From this, we can calculate a null expected Jaccard's similarity index (J_{exp}) (a similar approach can be used for other incidence-based dissimilarity metrics) by

$$J_{exp} = \frac{SS_{exp}}{\alpha_1 + \alpha_2 - SS_{exp}}.$$

When $\alpha_1 = \alpha_2$ for any given γ , the null expectation is an accelerating positive relationship between α and J_{exp} ; $J_{exp} = 1$ when $\alpha = \gamma$ (Fig.

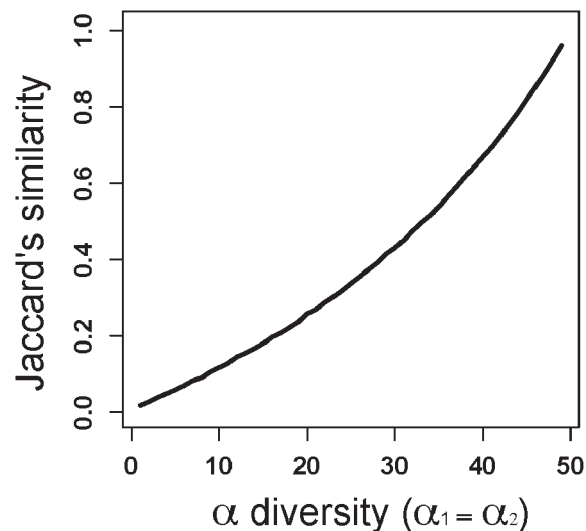


Fig. 1. The expected relationship between the local richness (α -diversity) in a pair of communities and the Jaccard's index of similarity (dissimilarity = 1-similarity), for the case where richness is equal in each local community ($\alpha_1 = \alpha_2$). Line traces the average of 999 replicates per α value, generated by sampling from a pool of 50 species with equal abundances.

1). When $\alpha_1 \neq \alpha_2$, a three-dimensional surface gives the null J_{exp} (not shown).

From Fig. 1, it is apparent how the most popular incidence-based metrics of dissimilarity (dissimilarity = 1 – similarity) that depend on SS_{obs} (e.g., Jaccard's and Sørensen's dissimilarity index, or other related metrics; e.g., Koleff et al. 2003) are strongly contingent on variation in α -diversity. When α is variable, for example when comparing among habitats or experimental treatments, or even when comparing among studies with different sample size, comparisons of incidence-based dissimilarity metrics cannot discern whether differences in dissimilarity are due to changes in the underlying structuring of community composition across sites, or instead simply due to changes in α -diversity. A null model approach can provide a straightforward way to discern whether species compositional differences among sites result from changes in α -diversity, or from forces causing communities to be more, or less, dissimilar than expected by random chance.

Estimating deviations from the null expectation

Given the three components of a diversity partition, α , β , and γ -diversity, a null model generally holds the values of two of those components constant (e.g., α and γ -diversity), and can be used to ask what the value of the third component (e.g., β -diversity) would be expected by random chance. A randomization test can then be used to compare the observed values relative to the expected values to detect deviations that would indicate changes in β -diversity that are not due to changes in α -diversity. These deviations can be in either direction, whereby β -diversity is either higher or lower than expected by chance given α -diversity and a regional species pool.

Although the exact form of the null model and associated tests will depend, to some degree, on the nature of the data and of the question being asked, the general principles are the same. For example, one could observe that average dissimilarity among pairs of local communities is greater for one group of communities than another, but if α -diversity was smaller among the more dissimilar communities, this result is expected by random chance alone (see Fig. 1). A null model is needed to discern whether the

difference in dissimilarity deviates from random expectation given the changes in α -diversity, and the results may indicate possible underlying mechanisms of community assembly. That is, communities that either are more, or less, similar than expected by chance can indicate some degree of determinism in the community assembly process (e.g., Chase 2007, 2010, Chase et al. 2009).

Here, we overview one method, known as the Raup-Crick metric (Raup and Crick 1979), that can provide some information on the degree to which pairwise communities are more different (or more similar) than expected by chance. As such, this metric allows one to develop hypothesis tests about the relative magnitude of the differences between observed and expected communities. Although the Raup-Crick metric was initially expressed as a similarity, we focus on it as a dissimilarity; to be consistent with the concept of β -diversity—we refer to this metric as β_{RC} (Vellend et al. 2007) (the R code we provide in the online supplement also allows the calculation of similarity if desired). In this case, rather than representing dissimilarity among pairwise communities per se, as in most metrics of β -diversity, the β_{RC} metric expresses dissimilarity among two communities relative to the null expectation. Specifically, if $SS_{1,2}$ is the observed number of shared species between localities 1 and 2, containing α_1 and α_2 species, respectively, β_{RC} uses a randomization approach to estimate the probability of observing $>SS_{1,2}$ given repeated random draws of α_1 and α_2 species from a known species pool (Fig. 2). For this null model to be most useful, knowledge of the species pool from which potential species are drawn is important.

In this section, we provide a step-by-step overview of the β_{RC} calculations. We do this because (1) the metric was introduced in the paleontological literature, and has rarely been used in ecology (a search of the ISI Web of Knowledge Science Citation Index database on 12/22/2010 shows fewer than 25 citations of the paper from ecological studies; <1 per year); (2) some of the decisions required to implement the calculations have not always been transparent, but can significantly alter the results; (3) the programs available for calculating the traditional Raup-Crick metric—PaST (Hammer et al. 2001)

and the current Vegan Package of R (Oksanen et al. 2011)—appear to have some critical limitations, which we address below. For any given α_1 and α_2 , β_{RC} compares SS_{obs} to the distribution of SS_{exp} values produced by a null model. We assume the use of presence-absence data. Although the β_{RC} calculation uses SS_{obs} and SS_{exp} , instead of a similarity metric, precisely equivalent results would be generated by any similarity metric based on SS_{obs} , such as Jaccard's or Sørensen's dissimilarity index. In the online supplement, we provide annotated R code that can be used to perform these analyses.

- *Step 1. Calculate the observed α_1 , α_2 , and SS_{obs} .* For any given pair of sites, α_1 and α_2 are the number of species observed in each site, and SS_{obs} is the number of species that the two sites share in common.
- *Step 2. Calculate the total number of species in the “species pool” among all sites, and the proportion of sites each species occupies (its “occupancy”).* These are calculated from all of the sites in the data set of interest (not just the two sites under consideration).
- *Step 3. Calculate the distribution of SS_{exp} values.* Randomly draw α_1 and α_2 species at random from the “species pool”. The probability of a species being drawn is proportional to its among-site occupancy. Repeat this procedure at least 1000 times (ideally more).
- *Step 4. Compare SS_{obs} with the distribution of SS_{exp} .* Sum the number of random draws in which $SS_{exp} > SS_{obs}$ and one-half of the random draws in which $SS_{obs} = SS_{exp}$, and divide the sum by the total number of random draws. This is an estimate of the probability of observing SS_{obs} or fewer shared species given random draws from the species pool.
- *Step 5. Standardize the metric to range from -1 to 1 .* Subtract 0.5 from the value from step 4, and multiply by 2.

Step 5 represents our primary modification of the original Raup-Crick metric (other than expressing it as a dissimilarity rather than similarity), by re-scaling it to vary from -1 to 1 . A value of 0 represents no difference in the observed (dis)similarity from the null expectation; a value of 1 indicates observed dissimilarity higher than the expected in any of the simulations (communities completely more different

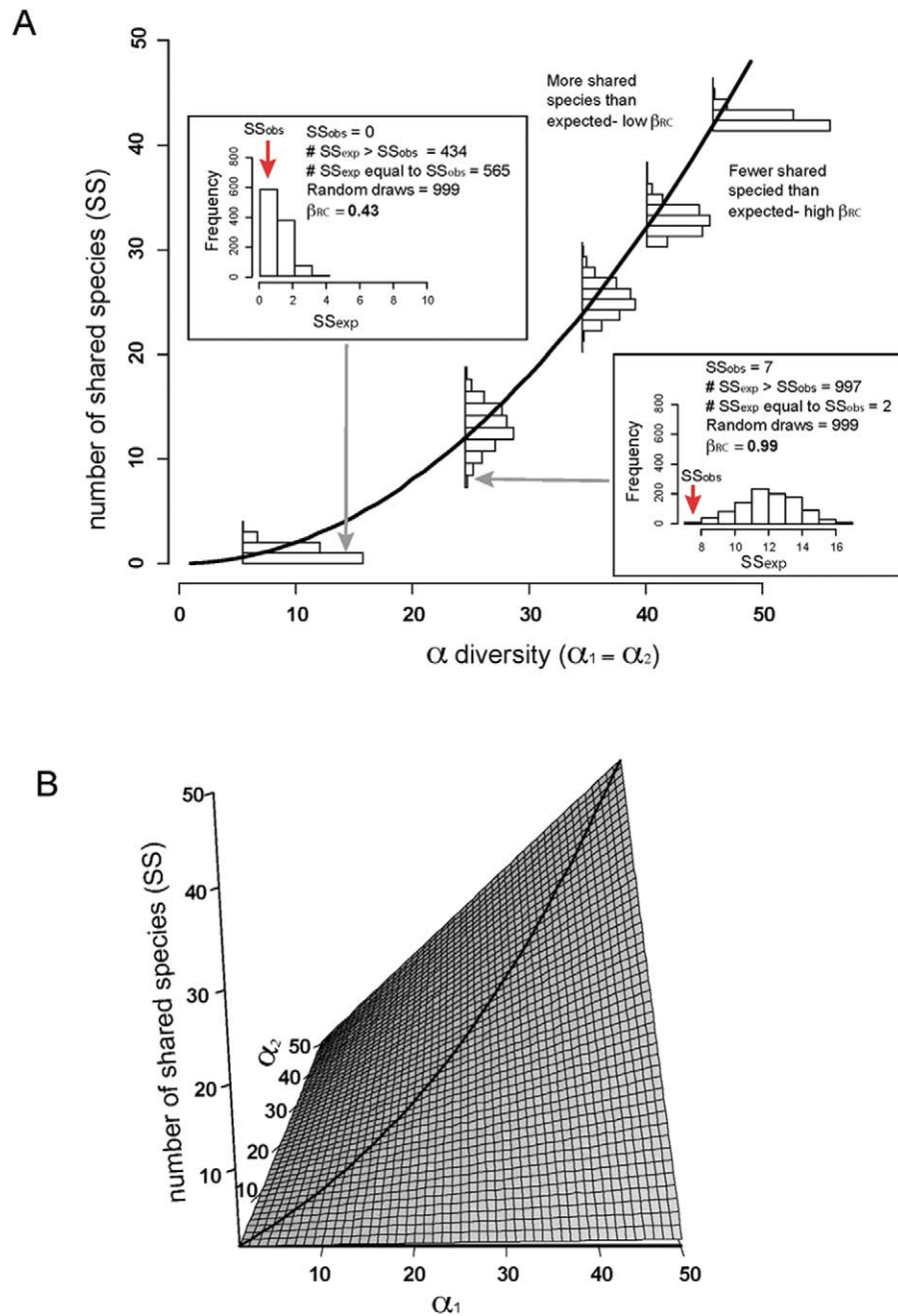


Fig. 2. The relationship between the local richness in a pair of communities (α_1, α_2) and the expected number of shared species between them (SS_{exp}) for a) the case where $\alpha_1 = \alpha_2$, and b) all possible combinations of α values, which produces a three-dimensional surface, but is otherwise the same as in panel a. The null expectation is shown as a solid black line in panel a, along with histograms showing the distribution of SS_{exp} for five values of pairs of α values (5, 25, 35, 40, 45) (based on 999 randomizations), demonstrating how the distribution is approximately normal when $\alpha = \gamma/2$, but has reduced variance and increased skewness as α approaches 0 or γ . Calculations for β_{RC} for two hypothetical cases of the observed number of shared species are shown. In the area below the solid line communities share fewer species than expected and therefore have high β_{RC} , while above the solid line more species are shared than expected, corresponding to low β_{RC} . These β_{RC} calculations are not shown in the three-dimensional version of panel b simply for clarity.

from each other than expected by chance), and vice versa for a value of -1 (communities completely less different [more similar] than expected by chance).

The main limitations of existing software implementations of the Raup-Crick metric are as follows: In the current Vegan package of R (Oksanen et al. 2011), the distribution of SS_{exp} is calculated analytically by a hypergeometric distribution. As such, every species in the regional pool is given equal weight, including species that are listed with zero abundances. Disregarding species frequencies has a large effect on value of the β_{RC} . It may be possible to use a Fisher noncentral hypergeometric distribution to incorporate a weighted species pool, however the simulation approach we take is more flexible. In the PaST (PAleontological STatistics) program (Hammer et al. 2001), it appears that steps 1–4 are identical to ours, except that a maximum of only 200 randomizations are performed in step 3. This limited number of randomizations results in low power to distinguish differences in the degree by which sets of communities that differ from the null expectation (e.g., when two groups of communities both differ from the null expectation, values of β_{RC} quickly converge on 1 [or -1] with fewer randomizations); this limitation is especially severe for species rich communities.

For our implementation of β_{RC} , one could ask whether SS_{obs} for a pair of communities is significantly different from the null expectation by assessing whether $|\beta_{\text{RC}}| > 0.95$ (two-tailed test, $\alpha = 0.05$). Such differences would indicate whether a given pair of communities share fewer (approaching 1) or more (approaching -1) species than expected by random chance. More commonly, however, values of β_{RC} are calculated for all pairwise combinations of communities, and these can be analyzed using the same set of statistical methods as the many other pairwise indices of dissimilarity (Tuomisto 2010a, b, Anderson et al. 2011).

Mean β_{RC} among habitats, experimental treatments, or time periods will be close to 0 when community assembly is highly stochastic and dispersal is high among communities, and will approach -1 when deterministic environmental filters shared across sites create highly similar communities (Chase et al. 2009, Chase 2010).

Alternatively, β_{RC} will be closer to 1 if deterministic environmental filters favor dissimilar species compositions, for example, if there were strong biotic structuring forces creating very different communities on adjacent sites (e.g., checkerboard distributions determined by competitive interactions; Diamond 1975), or if dispersal among sites is very low, leading to dispersal limitation.

It is worth noting that the influence of environmental filtering and dispersal limitation on β_{RC} (or any β -diversity metric) will depend on the sampling scale. If environmental filtering is strong, sites with similar environmental conditions should be more similar than expected ($\beta_{\text{RC}} < 0$), while sites with dissimilar environmental conditions should be less similar than expected ($\beta_{\text{RC}} > 0$). Likewise, when dispersal limitation is strong, nearby pairs of sites will be more similar than expected ($\beta_{\text{RC}} < 0$), whereas distant pairs of sites will be less similar than expected ($\beta_{\text{RC}} > 0$).

Caveats and considerations

β_{RC} is explicitly conditioned upon variation in α -diversity, and thus provides a more appropriate metric than other measures of dissimilarity for comparing the dissimilarity among communities that vary in α -diversity (e.g., Jaccard's or Sørensen's dissimilarity index). However, all metrics of β -diversity and associated null model analyses have limitations, and β_{RC} is no exception.

Specifying the regional species pool.—In practice, the species pool is typically characterized as the set of species (and their frequencies across localities) observed during the sampling of a given set of localities. However, the size of the pool will depend on the number of localities sampled (Gotelli and Colwell 2001), and correspondingly, the deviation of SS_{obs} from SS_{exp} will depend on the accuracy of the estimation of the species pool. Additionally, the choice of how to define the regional species pool will often have to be tailored to the question being addressed. For example, if within-habitat β_{RC} is being compared among habitats that differ in the set of species that can live there for deterministic reasons, the choice of whether to include only the species that live in a particular habitat type, or whether to include the species that live in each habitat type will strongly influence the value of the β_{RC} (see Gotelli and Graves 1996, Kraft et al. 2008,

Cornwell and Ackerly 2009 for related discussions). β_{RC} values will be closer to 0 (small deviation from the null-expectation) if the species from only that habitat are included in the species pool used to calculate SS_{exp} , relative to the case where species from multiple habitat types are included in the species pool. At the same time, it is not advisable to use a regional species pool that is so large (e.g., all of the species of a particular group across biogeographic zones) that all communities would have exceptionally low β_{RC} values. While resolution of the regional species pool issue is beyond the scope of the present paper, a simple ‘rule of thumb’ for including a species in the regional species pool to generate meaningful interpretations of β_{RC} would be to include those species that can possibly colonize a given site within a reasonable time period. Furthermore, it is worth keeping in mind that each alternative designation of the regional pool essentially asks a different research question, so therefore consistency or discordance in results among different pool designations (as well as those that do and do not disentangle α -diversity) can provide insight into ecological questions. For example, to examine the role of dispersal limitation in creating patterns of community dissimilarity relative to environmental features, one could compare whether community compositional dissimilarity deviates from the null expectation at relatively small scales (when the regional pool is constrained to that observed in a given set of sites) to the deviation obtained when the regional pool incorporates a larger number of species that could potentially colonize a site, but only very rarely do so. There are some instances where one might want to include species in the pool that are not observed in the sampled communities, but known to be present. The R-code we provide in the online supplement does not currently allow for the pool to be higher than those species that in at least one of the samples, but this could certainly be modified if the investigator feels that it is useful. However, we note that while increasing the size of the species pool will increase the absolute magnitude of the deviation from the null expectation, it will not generally influence the relative deviations among pairs of communities.

Species occupancies.—We suggest that the proportion of sites occupied by each species should

be incorporated into the null model calculations of SS_{exp} (though this can be bypassed in the R-code we provide) (see also Connor and Simberloff 1978, Raup and Crick 1979). If all species are considered equally likely to occupy a given site in the null model, SS_{obs} will often be much greater than SS_{exp} , and β_{RC} will be more negative (see Gotelli and Graves 1996, Kembel and Hubbell 2006, Hardy 2008 for related discussion). A potentially difficult question concerns how to incorporate occupancies of species when there are multiple habitat types (or treatments within an experiment). Species will likely vary in their degree of occupancy of patches across different habitat types, if, for example, a species occupies a large proportion of the available sites in habitats in which it is favored, and many fewer sites in habitats that it is less favored. Here, if one wants to include occupancies into the calculation of SS_{exp} , and include both habitat types, it would be essential to ensure a relatively equal sampling effort on both of the habitat types, so that occupancies would be representative of the entire region (Vellend et al. 2007).

Power to detect differences at low and high α -diversity.—Despite its advantages, β_{RC} , and in fact all pairwise dissimilarity metrics, suffer from some undesirable (and unavoidable) properties when α -diversity is either low or very high relative to the species pool. The problems stem from the fact that SS_{exp} must take an integer value, and the number of theoretically possible values of SS_{exp} can be quite small in some cases (Fig. 2a). For example, if $\min(\alpha_1, \alpha_2) = 5$, there are only six possible values of SS_{exp} : 0, 1, 2, 3, 4 and 5. For the hypothetical case where the number of species in the species pool is 50, $\alpha_1 = \alpha_2 = 5$, and species are equal in their occupancies of sites, the minimum possible SS_{exp} (0) is in fact a highly probable outcome of the null model (probability > 0.55). Thus, there is low power to detect any deviation from the null expectation in such cases. This is an inherent property of metrics that rely on species presence-absence information, and cannot be remedied by any kind of quantitative correction or analysis, but must be kept in mind when making such calculations. One solution is to down-weight the influence of any such values in downstream analyses based on the full matrix of pairwise dissimilarities.

An illustration of the utility of null models in β -diversity studies

To illustrate the importance of null models in addressing hypotheses regarding β -diversity and the possible mechanisms by which it is created, we show data from two disparate studies that both examined the effects of disturbance on patterns of community structure (Chase 2007, Anderson et al. 2011). In the first case, data were collected from experimental freshwater ponds, ten of which were controls, and ten of which were subjected to drought in the middle of the experiment (Chase 2007). Although drought decreased α -diversity somewhat (data not shown), it had a marked influence on β -diversity as measured using Jaccard's dissimilarity index, with ponds exposed to drought being much more similar to one another compositionally than control ponds (Fig. 3a). β_{RC} values on this dataset show that communities in the drought ponds were more similar than expected by chance relative to the control ponds (Fig. 3b), suggesting that changes in β -diversity were not simply due to a random influence of drought on species in each locality, and instead likely resulted because drought imposed a systematic ecological filter that removed a subset of species in each of the communities exposed to drought (Chase 2007).

In the second case, data were collected from 10 transects collected before and after an El Niño induced coral bleaching event from Indonesia (Warwick et al. 1990) and re-analyzed using a variety of β -diversity metrics in Anderson et al. (2011). Following the bleaching event, there was a marked decrease in α -diversity (data not shown), and a large increase in β -diversity, as measured using Jaccard's dissimilarity index (Fig. 3b). However, there were no differences in β_{RC} values before and after the bleaching event (Fig. 3d) (see also Anderson et al. 2011). The contrast between the results for Jaccard's dissimilarity index, which suggest a large increase in β -diversity after the disturbance, and the β_{RC} results, which suggest no change in β -diversity relative to the null expectation once the effect of disturbance on α -diversity was considered, emphasize the importance of this approach.

Comparing the effects disturbance in these disparate systems simultaneously using metrics that are α -dependent (e.g., Jaccard's dissimilarity index) and α -corrected (e.g., β_{RC}) allows one to

delve into the possible classes of mechanisms by which disturbance acts on these communities. In the coral reefs, disturbance appears to have acted primarily through random sampling effects, where there was no difference β_{RC} before and after the coral bleaching event. Alternatively, in the ponds, drought disturbance acted more deterministically, such that β_{RC} was considerably lower in the ponds that experienced drought relative to the control ponds. Similar inferences can be made when comparing patterns of β -diversity among communities that differ in other factors that may influence α -diversity, such as predators (Chase et al. 2009), pathogens (Smith et al. 2009), or productivity (Chase 2010).

CONCLUSIONS

Ecologists have become increasingly interested in the patterns of, and processes leading to, the site-to-site (or time to time) compositional differentiation among localities— β -diversity—but have also increasingly recognized problems with its definition and analysis (e.g., reviewed in Tuomisto 2010a, b). The β_{RC} approach allows one to disentangle variation in community compositional dissimilarity across sites from variation in the α -diversity of those sites as long as those sites are embedded in the same regional species pool. As such, the β_{RC} metric can be used to address the question ‘does the compositional variation among communities differ from a null-expectation?’ (Condit et al. 2002, Dornelas et al. 2006), and the related ‘to what degree do communities deviate from the null expectation, and how do abiotic or biotic factors influence this deviation?’ (e.g., Chase 2007, 2010, Chase et al. 2009, Smith et al. 2009).

Although we espouse the β_{RC} approach as a useful metric, there are several different ways to implement null models in order to make inferences about patterns of β -diversity. The specific form of the null model will depend critically on the question being asked, as well as the scope of the data being analyzed. The β_{RC} metric is appropriate when comparisons are made among communities that can reasonably be considered to be a part of the same regional species pool. However, when comparisons of β -diversity among biogeographic regions that vary in the size of the regional species pool (e.g., along

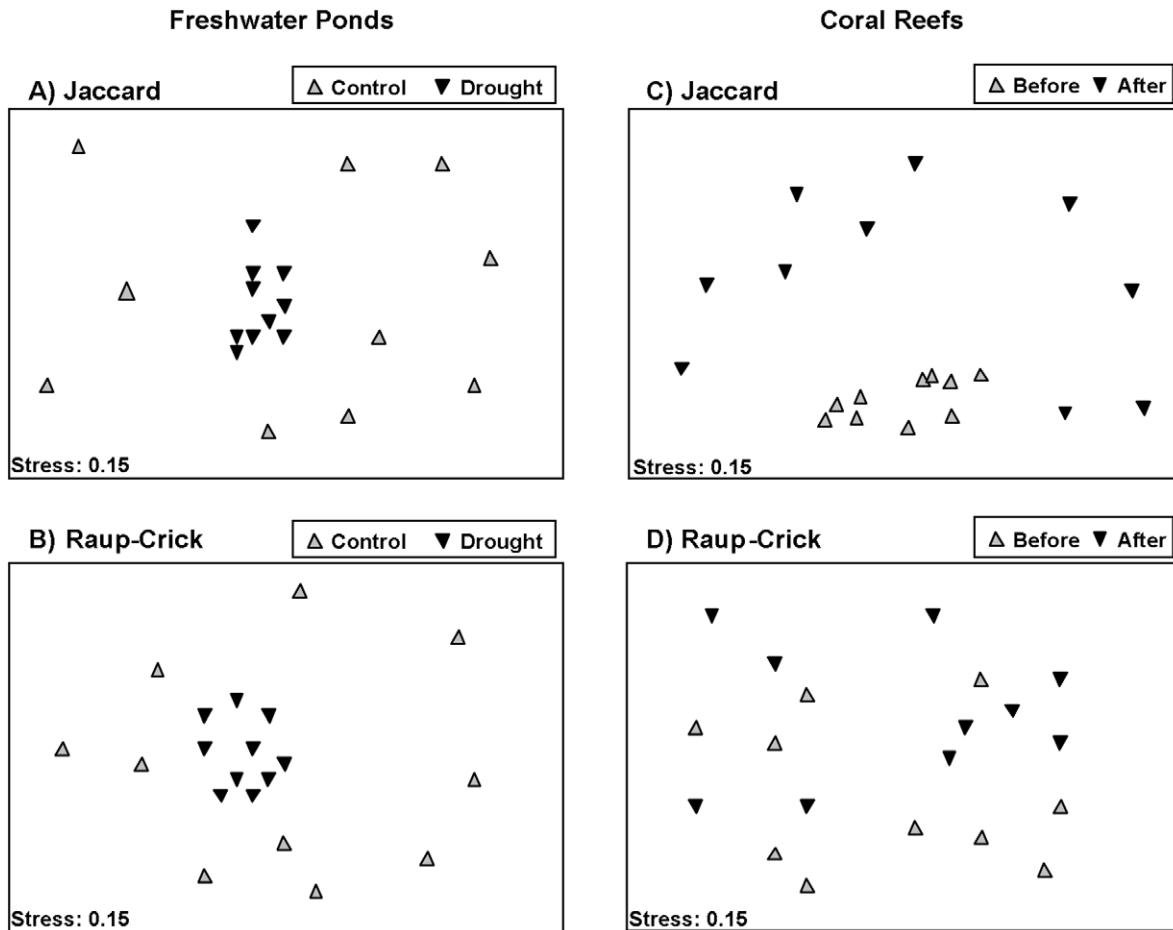


Fig. 3. Non-metric multi-dimensional scaling (MDS) ordinations based on Jaccard's Index (a, c) and β_{RC} (b, d) for two studies examining the effects of disturbance on patterns of β -diversity. Left panels (a, b) represent data from 20 experimental ponds, ten of which were subjected to experimental drought conditions, and ten of which were controls (data from Chase 2007). Right panels (c, d) represent data from ten transects of coral species composition from off of the Tikus Islands, Indonesia (data from Warwick et al. 1990) sampled prior to (1981) and following (1983) an El Niño bleaching event (modified from Anderson et al. 2011).

latitudinal gradients) are of interest, a related, but distinct null-modeling approach (e.g., Crist et al. 2003, Crist and Veech 2006) will be needed to disentangle the relative contributions of α -diversity and γ -diversity to variation in β -diversity.

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LITERATURE CITED

- Anderson, M. J. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19–28.
 Baselga, A. 2010. Multiplicative partition of true

- diversity yields independent alpha and beta components; additive partition does not. *Ecology* 91:1974–1981.
- Belmaker, J., N. Shashar, Y. Ziv, and S. R. Connolly. 2008. Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. *Ecology* 89:2829–2840.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences (USA)* 104:17430–17434.
- Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391.
- Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey communities. *Ecology Letters* 12:1210–1218.
- Condit, R. et al. 2002. Beta-diversity in tropical forest trees. *Science* 295:666–669.
- Connor, E. F., and D. Simberloff. 1978. Species number and compositional similarity of the Galápagos flora and fauna. *Ecological Monographs* 48:219–248.
- Cornwell, W. K. and D. D. Ackerly. 2009. Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs* 79:109–126.
- Crist, T. O., J. A. Veech, K. S. Summerville, and J. C. Gering. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* 162:734–743.
- Crist, T. O. and J. A. Veech. 2006. Additive partitioning of rarefaction curves and species-area relationships: unifying alpha, beta, and gamma diversity with sample size and habitat area. *Ecology Letters* 9:923–932.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Dornelas, M., S. R. Connolly, and T. P. Hughes. 2006. Coral reef diversity refutes the neutral theory of biodiversity. *Nature* 440:80–82.
- Freestone, A. L., and B. D. Inouye. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87:2425–2432.
- 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.
- Gotelli, N., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, D.C., USA.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1):9pp.
- Hardy, O. J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96:914–926.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Jost, L. 2010. Independence of alpha and beta diversities. *Ecology* 91:1969–1974.
- Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia* 159:15–26.
- Kemmel, S. W. and S. P. Hubbell. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* 87:86–99.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367–382.
- Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580–582.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Lepori, F. and B. Malmquist. 2009. Deterministic assembly peaks at intermediate levels of disturbance. *Oikos* 118:471–479.
- Leprieur, F., O. Beauchard, B. Hugué, G. Grenouillet, and S. Brosse. 2008. Null model of biotic homogenization: A test with the European freshwater fish fauna. *Diversity and Distributions* 14:291–300.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. *Vegan: Community Ecology Package*. R package version 1.17-7.
- Raup, D. M., and R. E. Crick. 1979. Measurement of faunal similarity in paleontology. *Journal of Paleontology* 53:1213–1227.
- Ricotta, C. 2010. On beta diversity decomposition: Trouble shared is not trouble halved. *Ecology* 91:1981–1983.
- Smith, K. G., K. R. Lips, and J. M. Chase. 2009. Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas. *Ecology Letters* 12:1069–1078.
- Tuomisto, H. 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1.

- Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2–22.
- Tuomisto, H. 2010*b*. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33:23–45.
- Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* 299:241–244.
- Veech, J. A., T. O. Crist, K. S. Summerville, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3–9.
- Veech, J. A. and T. O. Crist. 2010*a*. Diversity partitioning without statistical independence of alpha and beta. *Ecology* 91:1964–1969.
- Veech, J. A. and T. O. Crist. 2010*b*. Toward a unified view of diversity partitioning. *Ecology* 91:1988–1992.
- Vellend, M. 2001. Do commonly used indices of β -diversity measure species turnover? *Journal of Vegetation Science* 12:545–552.
- Vellend, M. 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* 85:3043–3055.
- Vellend, M., et al. 2007. Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *Journal of Ecology* 95:565–573.
- Warwick, R. M., K. R. Clarke, and Suharsono. 1990. A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8:171–179.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21:213–251.
- Wilson, M. V., and A. Shmida. 1984. Measuring beta-diversity with presence-absence data. *Journal of Ecology* 72:1055–1064.