



On the measurement of dimensionality of biodiversity

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ABSTRACT

Aim To characterize relationships among indices of taxonomic, phylogenetic, functional and phenetic diversity (TPFP diversity) for Neotropical bats and examine if dimensionality is different from null model expectations after controlling for sampling effects owing to underlying variation in species richness.

Location Neotropics.

Methods Bat distributions were estimated using geographic range maps. By overlaying range maps on a gridded map of the New World, the species composition of each cell was determined. Then, species richness and three indices each of phylogenetic, functional and phenetic diversity were calculated. A principal components analysis (PCA) determined the dimensionality of the entire multivariate data set. This was followed by two additional PCAs that examined the dimensionality of spatial and non-spatial fractions of the original data. Spearman rank correlations determined pair-wise association among indices. Correlations and dimensionality were compared with two different null models that account for species richness gradients.

Results Ten measures characterizing TFP diversity exhibited much spatial structure across the New World. Pair-wise correlations between indices were typically different from null model expectations. While patterns of multivariate covariation were similar across spatial and non-spatial data sets, the dimensionality of biodiversity was low and either lower than or no different from null model expectations.

Main conclusions Most measures of biodiversity exhibit at least some level of quantitative redundancy, and this redundancy is often higher than expected given sampling effects owing to species richness gradients. Considerations of uniqueness should be made when examining conceptually different dimensions of biodiversity.

Keywords

Dimensions of biodiversity, diversity gradient, functional diversity, phenetic diversity, phylogenetic diversity, taxonomic diversity.

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INTRODUCTION

Billions of years of environmental dynamics and biotic evolution have led to an almost unimaginably complex earth that teems with life. Despite centuries of documenting the world's biota we still know little about the spatial and temporal patterns of biodiversity and the mechanisms that generate them. Much of this ignorance stems from unidimensional approaches that have been used to try to understand what is in reality the multidimensional phenomenon of biodiversity (Stevens *et al.*, 2003,

2006; Stevens, 2011). For example, most research on broad-scale patterns of biodiversity has focused only on numbers of species (Willig *et al.*, 2003), a metric that while conceptually simple and intuitive ignores much of the complexity of life (Magurran & McGill, 2011). This is particularly unfortunate because a unidimensional approach could potentially underestimate current threats to biodiversity or stymie conservation efforts (Devictor *et al.*, 2010).

Ideas about the multidimensionality of biodiversity and the processes that generate and maintain it are longstanding (Noss,

1990; Zak *et al.*, 1994; Wiens, 2011). Fundamental ways to characterize the dimensionality of biodiversity are well known. Much attention has been given to taxonomic diversity, and research on functional and phylogenetic diversity has increased over the last few decades (Cisneros *et al.*, 2014). Less is known about variation in other complementary dimensions that have been described, and that include phenetic (Findley, 1973), interaction (Thompson, 1996) and character diversity (Williams & Humphries, 1996), as well as the concept of biological complexity (Naeem, 2001). Moreover, even basic information such as how fundamental dimensions are related to each other across empirical diversity gradients remains unclear.

Currently no synthetic conceptual framework exists that integrates variation across different dimensions of biodiversity. Correlations among some indices exist and in a number of situations are substantive (Devictor *et al.*, 2010; Stevens *et al.*, 2013). Nonetheless, such correlations are likely to be dependent on context, taxon and scale. Better understanding of the magnitude and variation in correlations and how they affect dimensionality is needed. Indeed, variation in the strength of correlation has substantive implications. For example, if variation in all indices across a number of dimensions of biodiversity is highly correlated, this suggests low dimensionality that is likely to result from one or a few mechanisms generating such variation. In contrast, low correlations suggest numerous independent axes of variation, and ultimately high dimensionality that can reflect different processes controlling the spatial patterns of variation of different dimensions of biodiversity. Several recent investigations have compared spatial or temporal variation in phylogenetic and functional dimensions of biodiversity and have found that they represent complementary perspectives (Meynard *et al.*, 2011; Strecker *et al.*, 2011; Swenson, 2013).

Despite complementarity, substantive correlations exist (Devictor *et al.*, 2010), and this is probably true for most if not all dimensions. One of the most important contributors to correlations among dimensions is the sensitivity of most indices to variation in number of items (i.e. species, ecological functions, alleles) owing to sampling effects. In particular, samples with greater species richness will express greater variability that manifests as higher magnitudes of indices measuring different dimensions of biodiversity. Thus, empirical diversity gradients should produce correlations among dimensions of biodiversity by virtue of changes in species richness alone (Naeem & Wright, 2003). Moreover, different dimensions are measured for the same entities (species) and this creates another form of non-independence that can reduce dimensionality.

When examining the dimensionality of biodiversity, the initial null hypothesis should perhaps be that dimensionality is no different from that expected given underlying variation in species richness. Moreover, because dimensionality has no straightforward a priori expectation, one starting point for better understanding its variation for a particular clade, spatial extent or ecological context is to address the question 'what is the expected dimensionality of biodiversity given the underlying variation in species richness?' In particular, if actual dimensionality is different from that expected based on the underlying

magnitude of species richness gradients, this suggests that more than the mechanisms controlling spatial variation in numbers of species will need to be understood in order to understand variation in biodiversity as a whole. More generally, significant deviations from expectations based on underlying variation in species richness warrant an explanation beyond that of simple sampling effects and in the direction of more sophisticated biological explanations.

Herein we characterize the patterns of biodiversity of noctilionoid bats distributed throughout the New World from the perspective of taxonomic, phylogenetic, functional and phenetic dimensions. We examine correlations among these different ways of estimating biodiversity and determine how dimensional such a multivariate data set is. Finally, we conduct null model analyses to evaluate if dimensionality is different from what would be expected given the underlying variation in species richness that characterizes spatial gradients of biodiversity for this important New World clade.

METHODS

The chiropteran super-family Noctilionoidea (*sensu stricto*: Noctilionidae + Mormoopidae + Phyllostomidae) is an ideal group for large-scale analyses of biodiversity. This clade of bats is of tropical affinity and has a long history of diversification in the New World (*c.* 49 Myr; Bininda-Emonds *et al.*, 2007). This superfamily is monophyletic (Teeling *et al.*, 2005), species rich (Willig & Selcer, 1989; Tello & Stevens, 2010) and phenotypically diverse (Baker *et al.*, 2003), and a well-resolved phylogeny exists characterizing evolutionary relationships among most extant species (Bininda-Emonds *et al.*, 2007).

Characterizing multiple dimensions of biodiversity

Patterns of diversity were characterized based on geographic range map overlaps (Patterson *et al.*, 2007, version 2) of 133 species. The continental New World was divided into 100 km × 100 km grid cells, and those species whose distribution overlapped a particular cell were included in the list of species for that cell. Only cells occupied by two or more taxa were considered in analyses. For each grid cell, we estimated taxonomic diversity as well as three indices each of functional, phylogenetic and phenetic diversity.

Taxonomic diversity

For taxonomic diversity we used number of species (taxonomic richness). This quantity is perhaps the most fundamental aspect of taxonomic diversity. We did not calculate indices that take into account evenness or dominance because available range maps provide no information on abundance of constituent species.

Phylogenetic diversity

For phylogenetic diversity we used the topology and branch lengths from the noctilionoid portion of the mammal supertree

of Bininda-Emonds *et al.* (2007). Based on this phylogeny, we calculated Faith's phylogenetic diversity measure (PD; Faith, 1992), phylogenetic species variability (PSV; Helmus *et al.*, 2007) and phylogenetic species clustering (PSC; Helmus *et al.*, 2007). PD measured the collective unique branch length of taxa within a grid cell. PSV characterizes relatedness among taxa across the entire phylogeny; it is directly proportional to the average pair-wise distance among species within a grid cell relative to a phylogeny (Helmus *et al.*, 2007). In contrast, PSC measures how clustered species are at the tips of the phylogeny; it is directly proportional to average nearest neighbour distance among taxa relative to a phylogeny (Helmus *et al.*, 2007). The supertree was manipulated in R using ape (Paradis *et al.*, 2004) and measures of phylogenetic diversity were calculated using PICANTE (Kembel *et al.*, 2010).

Functional diversity

We used the distribution of species across trophic guilds to estimate functional diversity. We were specifically interested in the diversity of explicit pathways whereby bats move carbon and energy through ecosystems (e.g. frugivory, insectivory, sanguivory) and categorized species into six functional groups based on diet: aerial insectivores, frugivores, gleaning animalivores, nectarivores, piscivores or sanguivores (Stevens *et al.*, 2003). Then we counted number of species per functional group within each grid cell and determined the richness of functional groups, the diversity of functional groups based on Shannon's index (Magurran & McGill, 2011) and the evenness of functional groups based on Camargo's index (Camargo (1993)).

Phenetic diversity

We characterized phenetic diversity based on seven morphological measures (Stevens & Willig, 2000): forearm length, greatest length of skull, condylobasal length, length of maxillary toothrow, breadth of post-orbital constriction, breadth of braincase and breadth across upper molars. Measures were based on the mean of at least four males and four females for most species. We log-transformed values for each morphological measure and then estimated three measures of phenotypic diversity for each grid cell. Morphological volume was estimated as the product of the ranges of all morphological variables (Ricklefs & Travis, 1980). Morphological variability was estimated by the standard deviation (STD) of the lengths of a minimum spanning tree uniting all species in multidimensional space (Ricklefs & Travis, 1980). The overall degree of proximity was estimated as the average distance of a species to its nearest morphological neighbour (Stevens & Willig, 2000).

Quantifying covariation among dimensions of biodiversity

We used a redundancy analysis (Legendre & Legendre, 1998) to examine the amount of variation in biodiversity indices among grid cells that could be accounted for by species richness. In this

analysis the nine other indices of biodiversity represented the dependent matrix and species richness represented the predictor variable. Similar univariate analyses were conducted for each biodiversity index using ordinary least-square regressions.

We examined the dimensionality of biodiversity from a multivariate perspective by calculating eigenvalues based on a principal components analysis (PCA) imposed on the 10 different indices of biodiversity. Because of nonlinear relationships among some indices (Fig. 1), the PCA was based on a Spearman rank correlation matrix. We used the 'Rnd-Lambda' stopping rule (Peres-Neto *et al.*, 2005) to distinguish eigenvalues that were larger than expected by chance and thus could be considered important axes of covariation among biodiversity indices. According to this approach, the original data matrix is permuted within variables (each index of biodiversity). A PCA is conducted and eigenvalues retained. This was repeated 1000 times to create distributions of eigenvalues for each principal component that would be expected if there were no relationships among variables. If an empirical eigenvalue was larger than the 95th percentile of the distribution of randomized eigenvalues, then that principal component was considered important. Each important eigenvalue represents a conservative measure of an orthogonal dimension of biodiversity.

We used the distribution of magnitudes of eigenvalues across all principal components as an overall measure of dimensionality. Multivariate data sets containing variables that are highly correlated exhibit low dimensionality. Also, such low-dimensionality data sets will yield a very uneven distribution of eigenvalues whereby most variation is accounted for by the first few derived (principal component) axes and the remainder account for little variation. In contrast, data that are highly dimensional will possess a number of uncorrelated variables. Eigenvalues will be more uniform, each accounting for similar amounts of variation. We used Camargo's evenness index (Camargo, 1993) to characterize evenness of eigenvalues.

Gradients underlying variation in biodiversity are inherently spatial phenomena. Thus we decomposed gradients into spatial and non-spatial components and evaluated the dimensionality of these two independent data sets. We used principal coordinates of neighbourhood matrices (PCNMs; Borcard & Legendre, 2002), based on the geographic coordinates of each grid cell, to characterize spatial relationships among sites. Then, we conducted a series of multiple regressions whereby each index of biodiversity represented the dependent variable and spatial PCNMs plus geographic coordinates represented the predictor matrix. The biodiversity values for each grid cell expected (i.e. predicted) from these regressions represented the spatially structured fraction of the data, whereas regression residuals of each measure represented the non-spatial (spatially unstructured) data. We then conducted PCA and determined the dimensionality for these two data sets according to the above methods. In total, we conducted three different PCAs: (1) ordinary PCA that examined the original data, (2) spatial PCA that examined only the spatially structured portion of the data and (3) non-spatial PCA that examined only the non-spatially structured portion of the data.

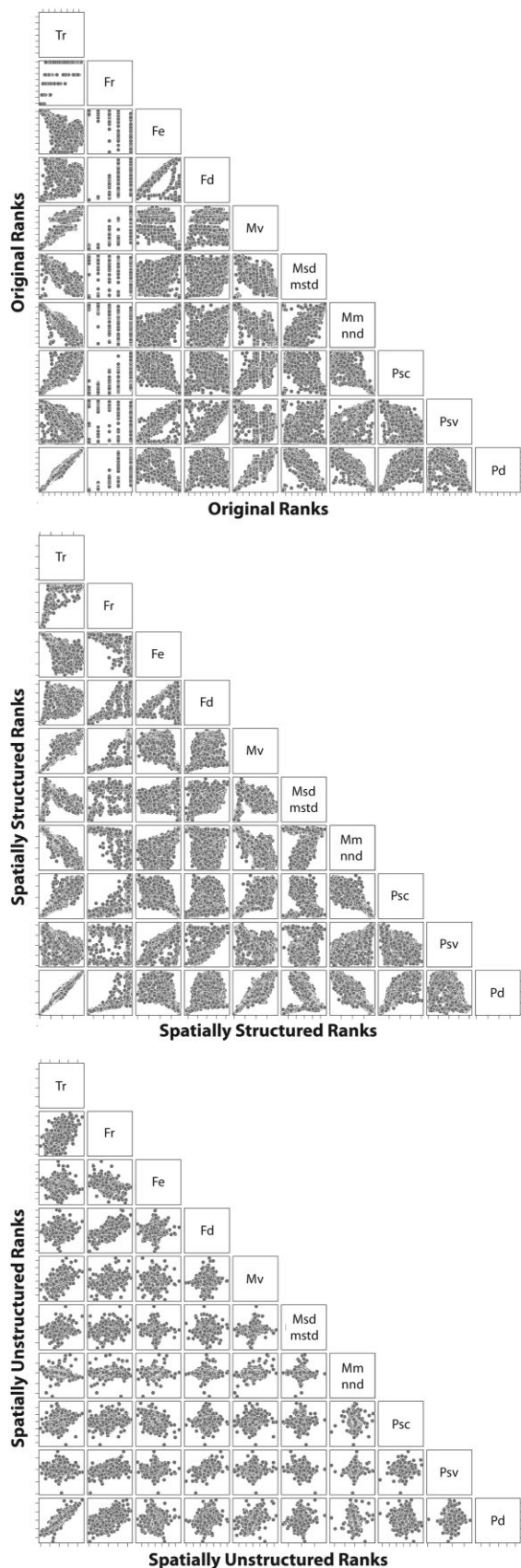


Figure 1 Scatter plots characterizing bivariate relationships among indices of biodiversity: (a) original data, (b) spatially structured data, (c) non-spatially structured data. Key: Tr, taxonomic richness; Fr, richness of functional groups; Fe, evenness of functional groups; Fd, diversity of functional groups; Mv, morphological volume; Msd mstd, standard deviation of morphological minimum spanning tree; Mm nnd, morphological mean nearest neighbour distance; Psc, phylogenetic species clustering; Psv, phylogenetic species variability; Pd, phylogenetic species diversity.

We were also interested in pair-wise patterns of covariation among biodiversity indices. For these we used a Spearman rank correlation coefficient to assess the magnitude of association between each pair of diversity indices; we did this for each data set (ordinary, spatially structured, non-spatially structured) separately.

Null models

We used two null models to generate expected values of biodiversity given the underlying number of species present in each cell. In the first null model (incidence-equiprobable), we constrained cells to have the same species richness as the empirical data but allowed any species to occur in them with equal probability (row sums fixed, columns equiprobable; Sim2 of Gotelli, 2000) by randomly sampling without replacement the same number of species found in the cell from the pool of New World Noctilionoidea. While such a null model ideally incorporates underlying spatial gradients in species richness, it ignores differences among species in the number of cells occupied (i.e. geographic range size). We conducted a more conservative null model (incidence-fixed) where both number of species per cell and number of cells occupied by species were maintained (row sums fixed, column sums fixed, occurrences randomly swapped; Sim9 of Gotelli, 2000). Indeed, numerous null scenarios exist to construct null models. Moreover in some cases, particular results depend on particular null models (Hardy, 2008). These two null models span the gamut from liberal (incidence-equiprobable) to conservative (incidence-fixed) and allow us to account for potential null model dependence.

To evaluate if the dimensionality of biodiversity was different from null model expectations based on underlying gradients of species richness, we compared the evenness of eigenvalues from the empirical PCA with a distribution of 1000 similar indices calculated on data generated from the null models described above. If the evenness index for the empirical data did not fall within the middle 95% of null distributions of indices, we concluded that dimensionality was different from that expected given sampling effects and the species richness gradient. To better explore which indices contributed to any significant difference, from the 1000 iterations of each null model we generated distributions of expected pair-wise correlations between indices of biodiversity (see Fig. S1 and S2 in Supporting Information).

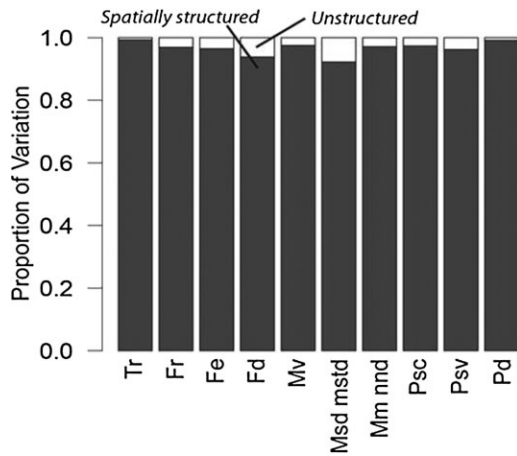


Figure 2 Decomposition of spatially structured and unstructured variation for each biodiversity index. Key as for Fig. 1.

Moreover, we evaluated if our results depended on the particular combination of indices used to measure diversity (Fig. S3)

RESULTS

Indices of biodiversity exhibited varying magnitudes of correlation (Fig. 1a) indicating redundancy across the empirical dimensions of biodiversity. Similar patterns of covariation exist for spatial and non-spatial data with the exception that correlations are typically weak across the non-spatial data (Fig. 1b, c). Most variation in biodiversity was spatially structured (Fig. 2). Although it varies among indices of biodiversity, non-spatial variation always represented a small fraction of variation accounted for. Species richness accounted for much of the variation among grid cells for different measures of biodiversity (Fig. 3). This was especially the case for the original data ($R^2 = 0.56$, $P < 0.001$) and the spatially structured data ($R^2 = 0.57$, $P < 0.001$). Even for the non-spatially structured data, species richness accounted for a significant amount of the variation in the indices of biodiversity ($R^2 = 0.16$, $P < 0.001$) but this was less so than for the other two data sets.

Only two important principal components characterized covariation in the original and spatial data sets (i.e. two significant PCs; Fig. 4) that accounted for approximately 82% of the variation in biodiversity. For these two data sets, indices of biodiversity exhibited both strong positive and strong negative correlations with the first principal component (Fig. 4a, b). Indices positively related to numbers of species such as richness, size of the morphological volume, Faith's phylogenetic diversity and phylogenetic species clustering were negatively related to the first PC. Indices more reflective of the similarity of items such as morphological mean nearest neighbour, standard deviation of morphological minimum spanning tree lengths and evenness of functional groups were positively related to the first PC. Indices exhibited either no correlation or negative correlations with the second PC (Fig. 4) and the diversity of functional groups exhibited the highest correlation with this axis.

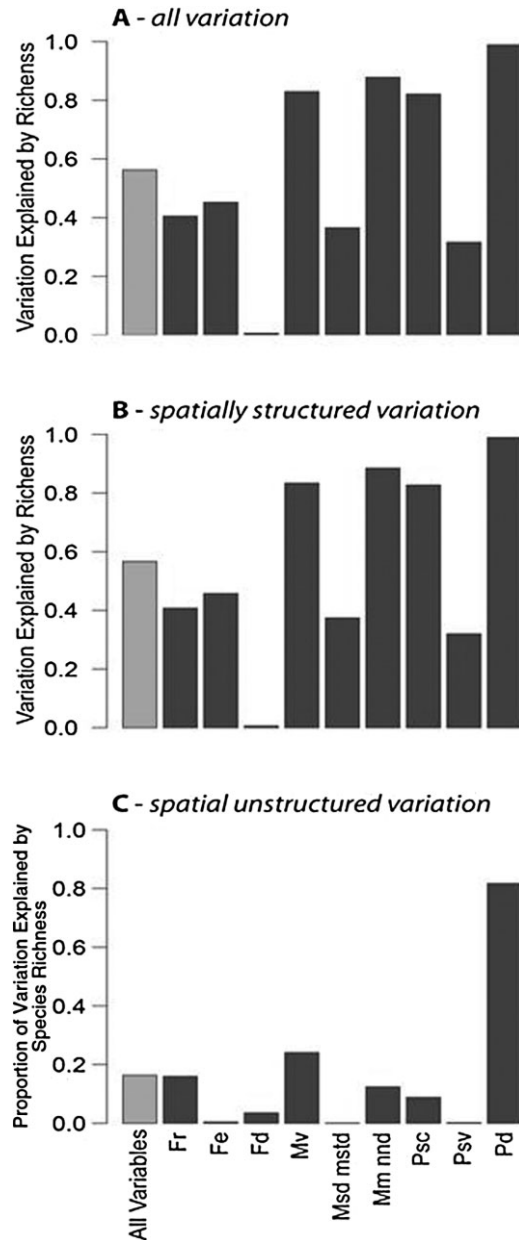


Figure 3 Variation accounted for by richness for original data (a), spatially structured data (b) and spatially unstructured data (c). The figure indicates the proportion of variation explained for each individual variable, as well as for the multivariate variation in biodiversity (excluding richness). Key as for Fig. 1.

PCA on the non-spatial data identified four important principal components that accounted for 74% of the variation (Fig. 4). Relationships between original biodiversity indices and the first two PC axes derived from this analysis were similar to those for ordinary and spatial data. In particular the first PC axis was strongly related to species richness, phylogenetic diversity, morphological volume and functional richness. The second axis reflected functional diversity, functional evenness and phylogenetic species variability. Unlike for the original and spatial data sets, the third and fourth principal components were

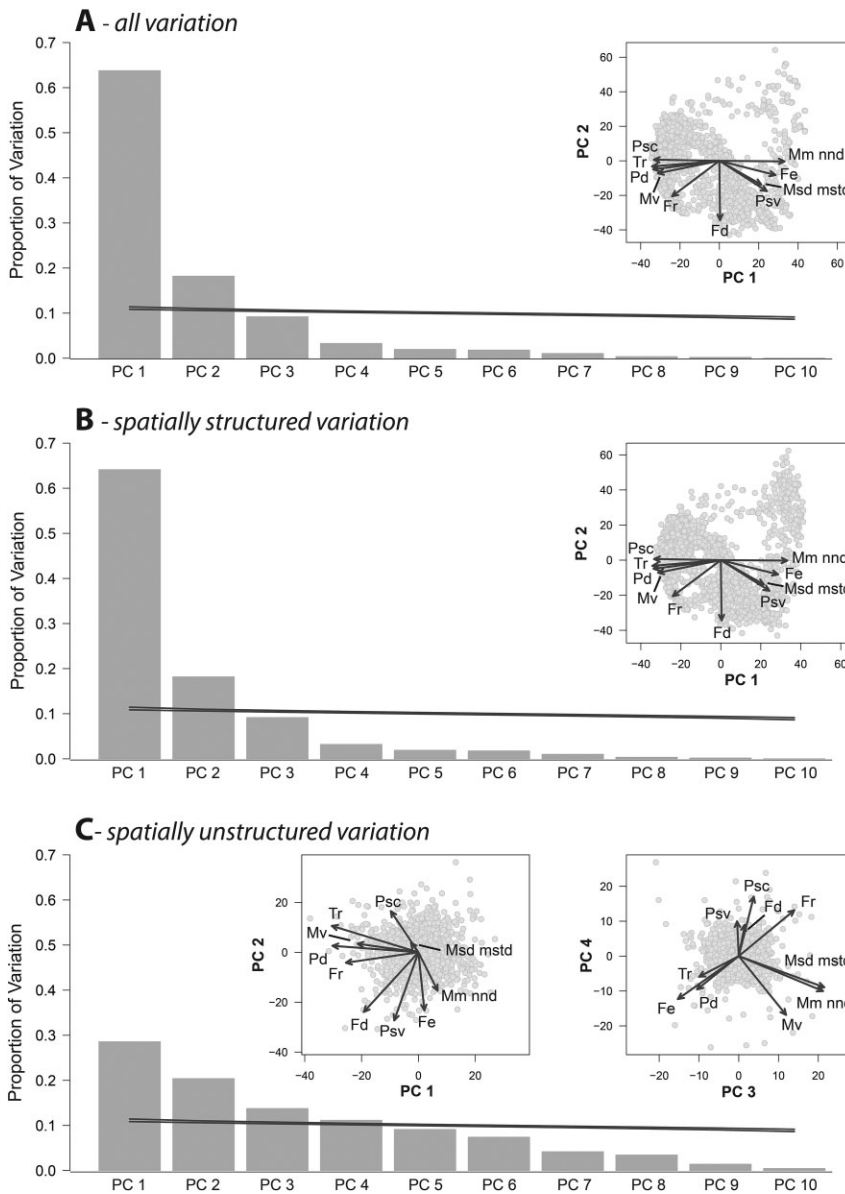


Figure 4 Results of principal components analysis (PCA) imposed on 10 indices characterizing four dimensions of biodiversity. In the main figure the height of each bar represents the amount of variation accounted for by each principal component (PC). The two horizontal lines represent the 95% confidence interval around the mean proportion of variance accounted for by each principal component when calculated on data that are permuted by the biodiversity index. If a particular principal component accounts for more the variation than that based on the permutation (if the histogram extends above the top line) then that principal component accounts for more variation than expected by chance and is considered statistically significant. PCA results for: (a) original data, (b) spatially structured data and (c) non-spatially structured data. The inset for each part shows loadings of 10 indices of biodiversity on principal components. Arrows represent the magnitude and direction of simultaneous correlations of each index with two principal components considered in the inset. Dots represent the position of each grid cell in this two-dimensional space. Key as for Fig. 1.

important too. The third axis characterized residual variation reflecting the tradeoff between functional evenness and clumping in morphological space. The fourth axis represented a different but related tradeoff between phylogenetic clumping and morphological dispersion.

Based on the original data set, significant differences existed between empirical evenness of eigenvalues and evenness calculated on eigenvalues generated from null model analyses (Fig. 5). Empirical dimensionality was significantly less than null model expectations. This was true for both null models. Nonetheless, empirical dimensionality was more similar to that produced by the incidence-fixed null model and quite different from patterns generated from the incidence-equiprobable null model.

When variation was decomposed into spatial and non-spatial data, dimensionality (evenness of eigenvalues) was greater for the non-spatial data than for the spatial data and this was true for both empirical and null model-based patterns. Moreover, for

both data sets empirical dimensionality was significantly different from dimensionality based on the incidence-equiprobable null model but not significantly different from dimensionality based on the incidence-fixed model.

DISCUSSION

Spatial variation in all measured dimensions of biodiversity was substantial for bats in the New World. Correlations among indices and dimensions were substantive. Moreover, such correlation indicates redundancy that reduces the dimensionality of biodiversity.

Main axes of variation in biodiversity of Noctilionoidea

Two important orthogonal derived axes of biodiversity exist for New World noctilionoid bats. Measures characterizing spatial

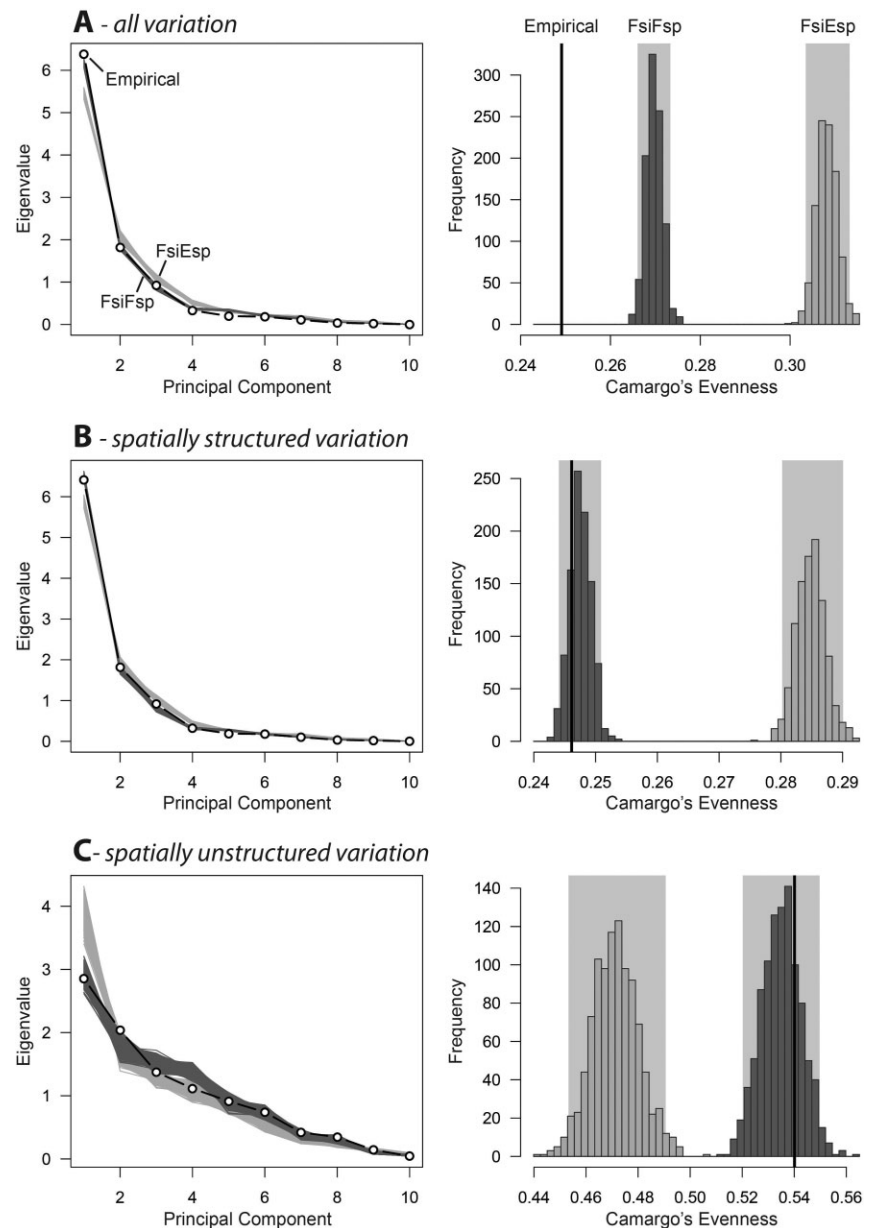


Figure 5 Results determining significant differences in multivariate dimensionality between empirical and null model generated biodiversity. Left: distribution of eigenvalues over 1000 runs of a null model. Light grey lines represent results from the incidence-equiprobable model, dark grey lines represent results from the incidence-fixed null model, and white circles and the black line represent results from empirical data. Right: comparison of empirical and null values of evenness among eigenvalues. The vertical line represents the empirical Camargo evenness calculated on eigenvalues for each of 10 principal components characterizing the empirical data (panels on the left). The light grey histogram characterizes the distribution of like evenness values generated from 1000 runs of the equiprobable-incidence random null model. The dark grey histogram characterizes the distribution of like evenness values generated from 1000 runs of the fixed-incidence null model. Rectangles behind each frequency distribution represents the area in which the central 95% of the null evenness values lie.

variation in volume along a particular dimension such as phylogenetic or phenetic diversity (i.e. size of the phylogenetic or phenetic space represented by an assemblage) were strongly and negatively related to this first dimension for ordinary, spatial and non-spatial PCs. In contrast, measures of dispersion were positively related to the first PC axis for ordinary and spatial PCs. As biodiversity increases with more and more species there is a reduction in the equitable distribution of items, and thus those indices that reflect variance are positively related to this primary dimension of biodiversity.

No clear grouping of variables by dimension type (i.e. taxonomic, phylogenetic, functional and phenetic diversity) emerges on primary axes of biodiversity as defined by PCA on any of the three data sets. When entities are even incrementally different, increases in the number of things will be a major contributor to

variability of items. That the axis of greatest variation in biodiversity is related to number of entities is likely to be very general. That different 'dimensions' of biodiversity, in particular taxonomic, phylogenetic, functional and phenetic diversity, are not orthogonal is not a new idea (Naeem & Wright, 2003; Helmus *et al.*, 2007). Nonetheless, one revelation of these analyses is that a greater understanding of dimensionality of biodiversity will perhaps come not from focusing on new conceptual dimensions drawn along lines of types of biological variability, such as taxonomic versus phylogenetic, but along even more general lines, in particular the statistical concepts of magnitude and distribution.

The second orthogonal derived axis of biodiversity of New World noctilionoids is that of functional diversity, represented for the most part by diversity of functional groups. This was true

for all three PCAs. Species are typically not uniformly distributed among ecological functions (Hooper *et al.*, 2005), and this non-uniformity is likely to decouple the relationship between diversity of functional groups and species richness. Indeed, species richness and functional diversity gradients are rarely linearly related to each other (Naeem & Wright, 2003; Cisneros *et al.*, 2014). Often there are more species than ecological functions, causing functional diversity to asymptotically increase with greater species richness. As species richness increases along a gradient, most functional groups are represented by relatively few species and further increases in richness serve to add taxa to pre-existing functional groups (Stevens *et al.*, 2003). Variation in diversity of functional groups is also likely to be less coupled to phylogenetic and phenetic diversity than are other measures of biodiversity. Most variation in phenetic and phylogenetic diversity is related to the addition of more functional groups, not adding to pre-existing functional groups. Form, function and phylogeny are intimately related (Ricklefs & Travis, 1994). Thus, an increase in number of functional groups also tends to add phylogenetically discrete ecomorphological groups. Accordingly, when a novel functional group is added to an assemblage this corresponds to the addition of a novel morphology or clade in a phylogeny with a substantive effect on all measures of biodiversity. Nonetheless, when species are added to pre-existing ecological functions this introduces more redundancy than novelty and serves to decouple diversity of functional groups from other measures of biodiversity. Indeed, fewer ecological functions than species and an unequal numbers of species per ecological function creates an important form of variation in biodiversity that varies orthogonally to variation in species richness.

Non-spatial data also possessed two additional important dimensions of biodiversity. The proportion of non-spatial variation was small (Fig. 2) and the third and fourth PC accounted for very few of these data. One obvious possibility is that these very small fractions of variation simply represent random noise or sampling error (Marcus, 1990). Nonetheless, these two axes accounted for more covariation than expected by chance and these two derived axes were related to how morphology is translated in terms of functional and phylogenetic diversity, respectively. Indeed, the major axis of variation in biodiversity in these data overall is related to species richness, and this variation is primarily spatial. Once this strong gradient is accounted for and residual variation in biodiversity is examined, the importance of other dimensions and their interactions is illuminated.

Dimensionality of biodiversity

Depending on the analysis, dimensionality was either lower or the same as expected given correlations of indices with species richness. In other words, most variation in biodiversity is related to and can be well characterized by patterns of species richness. One interesting pattern was that of significant differences between empirically generated dimensionality and that generated by null models. The difference was significant for the ordinary data set but non-significant for the spatial and non-spatial

data sets, at least for incidence-fixed scenarios. Moreover, dimensionality was significantly less than expected for the ordinary data set. Spatial and non-spatial data sets are unique additive fractions of the overall data set. For both the spatial and non-spatial data sets the main axis of variation was related to species richness, yet they each characterize a unique gradient describing variation in biodiversity. The combination of spatial and non-spatial gradients forming the original data set may serve to magnify the redundancy in biodiversity related to variation in species richness, thereby causing dimensionality to be lower than expected in the original data set.

Other phenomena also create redundancy and reduce dimensionality. For example, many new measures of biodiversity are often developed so as to be conceptually analogous to taxonomic diversity (Findley, 1973; Webb, 2000; Helmus *et al.*, 2007), in particular to express concepts of either species richness or evenness but measuring a different biodiversity dimension such as phylogenetic or functional diversity. This leads to measures that are sensitive to the same type of variation, namely the number or distribution of items in a set. We agree that variation in biodiversity cannot be encapsulated in a single variable (Gaston, 1996). Nonetheless, operationally, by developing new measures for unique dimensions based on the same concepts developed for taxonomic diversity, we are creating redundancy and potentially missing out on much of the diversity of life. What is needed is the development of concepts of biodiversity that, rather than reflecting numbers of things, reflect how biodiversity is distributed across complex dimensions. For example, focusing more on the distinctiveness (Clarke & Warwick, 2001) of species in an assemblage or even on the degree of correlation among characters may shed more light on variability and allow better characterization of the dimensionality of biodiversity.

A number of biological characteristics could also contribute to lowering the dimensionality of biodiversity. Null models that account for numbers of sites occupied by a species created patterns that were the least dimensional, with the exception of the non-spatial data. This reduced redundancy could at least in part be due to two aspects that are maintained in the fixed-incidence null models. The first are differences among taxa in range size. After numerous iterations of the equiprobable-incidence null models, random differences among taxa in their modelled range size disappear and range sizes of all taxa converge on the same mean. In contrast, fixed-incidence null models maintain differences among species in terms of the number of grid cells occupied. Extensive co-occurrence among widespread taxa may enhance redundancy, thereby reducing dimensionality. Indeed, fundamental gradients of biodiversity such as those for species richness are driven more by spatial variation in widely distributed species than by narrowly distributed species (Lennon *et al.*, 2004; Vazquez & Gaston, 2005). Moreover, distributions of widespread taxa are more related to the environmental characteristics underlying such gradients than are taxa of more limited distribution (Mora & Robertson, 2005; Tello & Stevens, 2010). Consistent with effects of widespread taxa may be an effect of another characteristic of the geographic range size distribution,

the average. Taxa with larger range sizes may exhibit a lower dimensionality of biodiversity than taxa with a smaller average range size. Thus, reductions in dimensionality may be further heightened for bats because of their relatively large range size (Villalobos & Arita, 2013). Species with extensive overlapping ranges are likely to make a smaller contribution to spatial variance than species with smaller more geographically idiosyncratic distributions.

Biodiversity is created by diversification, and this process is likely to be another important generator of variance. Nonetheless, some important characteristics of this process may also reduce dimensionality of biodiversity. Since two sister taxa inherit characteristics from a common ancestor, they themselves are redundant. Niche conservatism creates redundancy across the entire phenotype, and as a result affects dimensionality (Wiens, 2011). Moreover, sister taxa are often geographically distributed in close proximity (Rundle & Nosil, 2005), thereby compounding both phylogenetic and spatial non-independence, increasing intercorrelations and reducing dimensionality. Further contributing to this is the lack of independent spatial distribution that is caused by environmental gradients. Most species are distributed across many sites along a gradient. Accordingly, species co-occur with others even if they all exhibit different environmental optima. Recent approaches combining phylogenies with distribution patterns have demonstrated that while considerable variation exists in terms of the species composition of sites along environmental gradients, species that co-occur are often more closely related phylogenetically than those that do not (Cavender-Bares *et al.*, 2004), especially at high levels of species richness (Stevens *et al.*, 2012). Thus, how species respond to environmental gradients, in particular similar distributions of closely related species caused by niche conservatism, may substantially decrease the dimensionality of biodiversity.

Despite our findings of low dimensionality, we recognize the importance of using multiple indices to characterize biodiversity. We do not believe that phylogenetic, functional, phenotypic and taxonomic indices are fully redundant and that biodiversity can be characterized solely by species richness. Our results also demonstrate some complementarity. We found that at least two orthogonal axes are needed to describe the covariation among the biodiversity indices we used. Moreover, 16% of the multivariate variation in our original data set could not be included in the two significant principal components and represents variation that is unique to individual biodiversity indices. Discrepancies in variation among multiple indices of diversity can be very informative, allowing the development of predictions regarding mechanisms behind the structure of local and regional species assemblages (Davies & Buckley, 2011; Swenson, 2013). These discrepancies can also be used to highlight areas that could be of particular interest for conservation, where the maintenance of high numbers of species does not guarantee the conservation of high phylogenetic, functional or phenetic diversity (Devictor *et al.*, 2010). A multivariate and multidimensional approach to the study and conservation of biodiversity is fundamental.

Caveats

While examination of dimensionality can provide valuable insights, some caveats should be made explicit. First, as with many aspects of biodiversity, dimensionality is likely to be dependent on scale, taxon and ultimately context. While such dependence presents a challenge to making generalizations, it is these very differences that generate a more comprehensive understanding of how biodiversity varies in nature. Indeed, ecologists should embrace such dependence and make comparisons across many different contexts in order to better understand when dimensionality should be expected to be high or low.

A second caveat has to do with the diversity indices that are selected to characterize dimensionality. Indeed, a plethora exists and no study has ever examined all indices simultaneously. Thus, to some extent inference made on dimensionality is limited by selection of a particular subset of indices. This problem is not new and is true of any inference gathered from studies that do not use exactly the same indices. An insight from these analyses is that because most indices are correlated, the addition of more indices to analyses is likely to add unique variation only asymptotically; there are diminishing returns from adding diversity indices to analyses. One strength of these analyses is that inference is made relative to species richness, and thus provides insight into dimensionality relative to this baseline. Adding conceptually unique dimensions (i.e. phylogenetic, genetic, etc.) probably adds relatively more to dimensionality than does adding indices within particular dimensions. To this end the most meaningful analyses will come when studies share and compare the same conceptual dimensions of biodiversity.

Lastly, our analyses only address a spatial dimension. Variation in biodiversity forms a single, spatio-temporal continuum (Adler *et al.*, 2005), and while two or more indices may be highly correlated in space they may exhibit complementary relationships through time, and vice versa. Future analyses should examine similar patterns of redundancy through the temporal dimension. Moreover, spatial and temporal comparisons may provide insights into the exact context in which redundancy diminishes the dimensionality of biodiversity.

Conclusions

In this paper we have presented a new method to quantitatively assess the dimensionality of biodiversity and found that it is surprisingly low, particularly relative to expectations based purely on sampling effects due to species richness gradients. Although our analyses were not exhaustive in terms of indices, most spatial variation can be fairly well characterized by a few axes of covariation, especially if nonlinearities are accounted for. New concepts are needed to better characterize biodiversity, i.e. ones that describe the variability of life over and beyond simply reflecting number of entities in a set. Only then will greater complexity be appreciated and will more comprehensive conservation strategies than maximizing numbers of species be possible.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Results of equiprobable-incidence null model analyses for pairwise correlations among indices.

Figure S2 Results of fixed-incidence null model analyses for pairwise correlations among indices.

Figure S3 Results of sensitivity analyses confirming that any subset of biodiversity indices would lead to the same conclusion reached with the full set presented in the body of the manuscript.

BIOSKETCHES

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