

Decomposing functional diversity

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Summary

1. One aspect of biodiversity, functional diversity, reflects the functional role of species within a community as measured by species characteristics. We present a new metric, functional trait dispersion, based on the concept of species distinctiveness measured as the distance among species in the multidimensional space defined by trait values. This metric can be decomposed into components of species richness, functional evenness and mean dispersion, and into parts that measure diversity within and among subgroups.

2. Using an appropriate distance measure, mean dispersion (M') is calculated as the average distance among all possible pairs of species. Functional evenness [${}^qE(T)$] is derived from Hill diversity based on the proportional distances between pairs of species and species richness (S). Functional trait dispersion [${}^qD(TM)$] is then computed as $1 + (S-1) \times {}^qE(T) \times M'$. It has a range of $[1, S]$ and measures the effective number of functionally distinct species for a given level of species dispersion.

3. Using constructed data, we demonstrate that ${}^qD(TM)$ captures appropriate ecological properties such that a community with greater species richness, greater dispersal in trait space or greater mean dispersion has greater functional diversity. Functional trait dispersion can also provide measures of within-community dispersion and the effective number of functionally distinctive compartments (groups of communities with similar functional structure). Using empirical data of bats along an elevational gradient in Peru, we demonstrate that functional trait dispersion and its components provide insights about gradients of biodiversity.

4. Functional trait dispersion comports to reasonable criteria for a metric of functional diversity and can be decomposed in a variety of ways that facilitate understanding of patterns of variation. Other metrics of functional diversity neither integrate all three diversity components, nor can many be decomposed into variation within and among subgroups. Because functional trait dispersion measures properties of distance and the effective number of functionally distinct species, it can be used in conjunction with other biodiversity metrics that are based on species identity, abundance or phylogenetic relatedness to inform management and the preservation of biodiversity.

Key-words: alpha diversity, bats, beta diversity, dispersion, diversity metric, evenness, functional trait, gamma diversity, Hill diversity, Peru, species richness

Introduction

The diversity of a biological community can be measured in a variety of ways, each of which captures information about a different aspect of species within that community. Here we consider the functional diversity of species, which are a natural focal unit for communities, although other foci can be considered such as genes or traits. Differences among members of a community may be reflected in their taxonomic identities, abundances, phylogenetic relationships or functional characteristics. Until recently most measures of diversity focused on species identities or abundances (Magurran & McGill 2011). In the past two decades attention has expanded to include aspects of phylogeny (e.g. Faith 1992; Chao, Chiu & Jost 2010)

or function (Table S1, Supporting Information). Interest in functional diversity has increased markedly in the past few years, with considerable focus on how it should be measured and in the number of studies using those metrics (Reynolds *et al.* 2015). In this paper, we examine the concept of functional diversity, propose a metric that integrates its multiple aspects, and compare that metric to ones that are used most commonly.

Functional diversity is a complex concept, much more so than identity, abundance or phylogenetic diversity. Identity diversity is species richness. Abundance diversity characterizes each species by its proportional abundance, recognizing that other units such as biomass or frequency of occurrence could be substituted for abundance. Although many metrics of abundance diversity have been proposed (see Table 9.2 in, Gurevitch, Scheiner & Fox 2006), many are special cases of the Hill index (Hill 1973):

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[Correction note: The Supporting Information was modified on 20 February 2017.]

$${}^qD(A) = \left(\sum_{i=1}^S p_i^q \right)^{\frac{1}{1-q}} \quad \text{eqn 1}$$

and

$${}^1D(A) = \lim_{q \rightarrow 1} {}^qD(A) = \exp \left(- \sum_{i=1}^S p_i \log p_i \right), \quad \text{eqn 2}$$

for non-negative $q \neq 1$ and $q = 1$, respectively, where S is the number of species, p_i is the proportional abundance of the i th species, q is the order of the diversity metric that determines the weighting of proportional abundances and A indicates that diversity is measured based on abundances. The index has a range of $[1, S]$ and measures species equivalents. It measures the effective number of species that a community would contain if it had the same diversity and all species had the average abundance. Values of 0, 1 and 2 for q are common and associated with popular metrics. When $q = 0$, ${}^0D(A)$ equals species richness; when $q = 1$, ${}^1D(A)$ is the exponential of Shannon diversity; and when $q = 2$, ${}^2D(A)$ is the Gini–Simpson index (Hill 1973; Chiu, Jost & Chao 2014). As the value of q increases, the relative contributions of more abundant species increase. Measured in this way, diversity comprises two components, richness and evenness: ${}^qD(A) = S \times {}^qE(A)$ (Tuomisto 2012). An analogous measure of phylogenetic diversity based on the relative branch lengths of each species reflects the number of equally divergent species (Scheiner 2012). This metric also comprises components of richness and evenness. Because abundance and phylogenetic diversity are measured in species equivalents, comparisons are facilitated among communities and between measures of diversity based on different types of species characteristics (e.g. abundance, evolutionary history).

Abundance and phylogenetic diversity are each based on a single characteristic of each species. In contrast, functional diversity is typically based on multiple traits of each species. Previously, we (Presley, Scheiner & Willig 2014) defined a metric of functional diversity based on the Hill index. That metric captured two components, richness and functional evenness, expressed as the number of equivalently distinct species from a functional perspective, making it analogous to Hill diversity as measured for abundance or phylogeny. However, that measure of functional diversity only reflects the evenness of the distribution of species in trait space. Functional diversity has another characteristic, the magnitude of dispersion of species in trait space. Here, we produce an integrated measure that combines richness, evenness and dispersion into a single metric, functional-trait dispersion.

Functional diversity

CONCEPTS

Functional-trait dispersion is based on the concept of distinctiveness as measured by the distance among species in multidimensional trait space. For categorical traits, functional diversity can be defined based on one of these two concepts:

1 Functional diversity is greatest when each species in an assemblage has a unique set of trait attributes.

2 Functional diversity is greatest when an assemblage contains species that have every possible combination of trait attributes.

For simplicity, we label these the ‘uniqueness’ and ‘combinatorics’ concepts respectively. Our metric is based on the uniqueness concept; many other metrics are based on the combinatorics concept (see below). The uniqueness concept for continuous traits posits that maximum diversity corresponds to each species occurring at the boundary of trait space and being equally as far apart from each other as possible. For the combinatorics concept, maximal diversity occurs when the dispersion of species is as compact as possible while equalizing the minimum distances between species (Fig. 1).

A metric of functional diversity should be able to distinguish between communities of species that differ in several properties that emerge from the uniqueness concept. For two communities, functional diversity should be larger for the community that has a greater dispersion of species in the trait space, a more equitable distribution of species in trait space (evenness) or greater species richness. Consequently, an integrated metric should combine the properties of dispersion, evenness and richness, and be decomposable into those separate components. Moreover, the metric should facilitate the separation of functional diversity with respect to a hierarchy, that is a larger unit such as a landscape (γ -diversity) into the mean functional diversity of constituent subunits such as local communities (α -diversity) and to variation among those subunits or local communities (β -diversity). Finally, a metric of functional diversity should not be confounded by considerations of other properties of species, such as abundance or phylogenetic distance, but should facilitate integration with other properties into a more comprehensive metric.

When functional diversity is based on the dispersion of species in trait space, it is a measure of the way that species characteristics affect the role of a species within a community (‘function of’). This aspect of functional diversity is closely related to concepts of the niche (Chase & Leibold 2003). In contrast, a metric can reflect ‘function for’, the way that each species affects ecosystem properties (e.g. the amount of carbon fixed per unit area per unit time). It is possible to measure function-for diversity as species equivalents (Scheiner 2012), and discussions of functional diversity are typically couched in

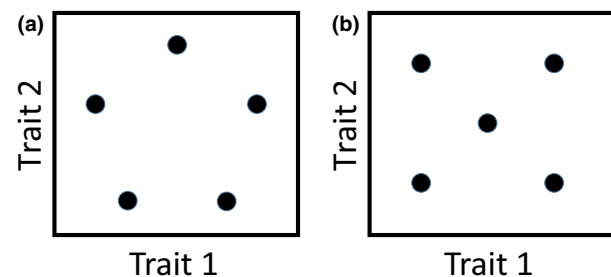


Fig. 1. Graphic representation of the position of five species in functional space defined by two traits. (a) An illustration of the uniqueness concept where each species has the same set of distance with all of the other species and are as distant from each other as possible. (b) An illustration of the combinatorics concept where each species has the same minimum distance, in this case the distance to the central species, in as compact an arrangement as possible.

attempts to understand the ways that diversity affects ecosystem processes (Tilman *et al.* 1997; Hooper *et al.* 2005; Nunes-Neto, Moreno & El-Hani 2014; Mokany *et al.* 2016). However, function-for is difficult to measure, so research efforts generally focus on function-of, an exception being Cadotte *et al.* (2009). Generally, function-of is assumed to be a proxy of function-for. We focus on diversity that reflects function-of and leave the chore of linking diversity with function-for to a later endeavour.

COMPONENTS

Measures of abundance and phylogenetic diversity based on Hill numbers have two components – richness and evenness – embodied in a multiplicative relationship, diversity = richness \times evenness (Jost 2006; Scheiner 2012). For functional diversity based on trait values of species, the central properties to capture are the configuration and dispersion of species in trait space. Consequently, considerations of trait space require concepts of richness and evenness that are different from those used with regard to abundance or phylogeny.

Mason *et al.* (2005) recognize three components of functional diversity: functional richness, functional evenness and functional divergence (we prefer to restrict the term ‘divergence’ to characterize phylogenies, and recommend ‘distinctiveness’ to characterize function). In their lexicon, functional richness is the amount of trait space occupied by species; functional evenness is the equability of abundances in trait space; and functional distinctiveness is the dispersion of species in trait space weighted by their abundances. Of the many metrics that have been proposed, six are most commonly used (Reynolds *et al.* 2015): richness as FD or FRic, evenness as FEve and distinctiveness as Rao’s Q, FDis or FDiv (Table S1). We consider two additional metrics. Functional attribute diversity (FAD) is a measure of functional distinctiveness, and is the original functional diversity metric. Total functional diversity, ${}^q\text{FD}$ (Q), has been proposed recently and is the only metric that combines richness, evenness and abundance-weighted dispersion.

The weighting of trait values by abundance is based on the assumption that function-for has a linear relationship with species abundances. However, such weighting confounds function-of with function-for. Importantly, there is no justification for assuming that function-for effects will scale linearly with abundance or that such scaling will be the same for all species. Even within a group of closely related and morphologically similar species such as New World bats, body mass can range from 5 to 190 g. Food consumption or seed dispersal by ten individuals of a large canopy frugivore (e.g. *Aribeus lituratus*, 60.3 g) is unlikely equal to food consumption or seed dispersal by ten individuals of a small canopy frugivore (e.g. *Mesophylla macconnelli*, 6.9 g). Consequently, one could argue that trait values should be weighted by the cumulative mass of a species rather than by its abundance, and even this assumes that metabolic constraints are equivalent for all species. Such weighting of trait values is arbitrary unless accompanied by a cogent conceptual justification or empirical measures that corroborate ecosystem consequences.

We take a different approach to richness, evenness and distinctiveness as it relates to functional diversity. Rather than considering functional richness as a property of how trait space is filled as per Mason *et al.* (2005), in our metric functional richness is linked to species richness so that the integrated metric measures quantities of distance and the effective number of functionally distinct species and scales with species richness. We define evenness, ${}^qE(T)$, as the extent to which species are equally dispersed in trait space. Functional-trait species diversity, ${}^qD(T)$, is based on variation in dispersion and uses the Hill number framework, so it combines richness with evenness (Presley, Scheiner & Willig 2014). We define dispersion as the mean distance between all pairs of species in trait space. Our measure of functional diversity – functional-trait dispersion – integrates these properties in a multiplicative way so that diversity increases with the product of richness, evenness and dispersion. This relationship, thus, has a direct parallel to multiplicative measures of abundance and phylogenetic diversity. Importantly, our metric of functional diversity measures meaningful properties of communities independently of species’ abundances.

Our concepts most strongly diverge from those of Mason *et al.* (2005) with regard to evenness. Ignoring considerations of abundance, for them species are most evenly dispersed in trait space when each species has the same distance to its nearest neighbour (Fig. 1a). For us, species are most evenly dispersed when each has the same distance to all other species. For continuous traits, maximal evenness can occur only when the number of species is less than or equal to the number of traits plus 1. Otherwise, it occurs when species are arrayed in trait space so that each species has the same relationship with all other species and consequently the same set of distances (Fig. 1b). Their approach is based on a combinatorics concept, whereas our approach is based on a uniqueness concept.

CONSTRUCTING THE DIVERSITY METRIC

Let d_{ij} represent the standardized distance in trait space between the i th and j th species, so that $0 \leq d_{ij} \leq 1$, $d_{ij} = d_{ji}$ and $d_{ii} = 0$. The mean of those distances for all species is: $M = \sum_i^S \sum_j^S d_{ij} / S^2$, where S is number of species. M provides a measure of the magnitude of dispersion; it has a range of $[0, (S-1)/S]$ and measures standardized distance.

We next define the proportional distance between the i th and j th species as $f_{ij} = d_{ij} / \sum_j^S d_{ij}$. Using that, we obtain a measure of variability among pairwise distances with the Hill function (Hill 1973):

$${}^qH(T) = \left(\sum_i^S \sum_j^S f_{ij}^q \right)^{\frac{1}{1-q}}, \quad \text{eqn 3}$$

(by definition ${}^qH(T) = 0$, if all $d_{ij} = 0$). From this quantity we calculate functional-trait species diversity:

$${}^qD(T) = \frac{1 + \sqrt{1 + 4{}^qH(T)}}{2}. \quad \text{eqn 4}$$

The derivation of this metric is given in the Appendix S1. This metric indicates the effective number of equally distant

species and has a range of $[1, S]$. ${}^qD(T)$ is maximized at S when all species are equidistant in trait space; ${}^qD(T)$ can equal S only if the number of species do not exceed the number of traits plus 1. Otherwise, the effective number of species is less than S , and equals the number of species whose pairwise distances would sum to the total pairwise distance if all interspecific distances exactly equal the weighted generalized mean of pairwise distances with exponent $q-1$ (see the Appendix S1 for a derivation of this definition, eqs. A8 and A13). As the evenness of the distribution decreases, ${}^qD(T)$ decreases. The greater the value of q , the more weight is given to pairs of species with large distances. This effective number is directly analogous to that for abundance data (eq. 1). Similar to abundance diversity, a limit formulation (eq. 2) is used when $q = 1$. ${}^qD(T)$ can be decomposed into components of richness and evenness: ${}^qE(T) = {}^qD(T)/S$ (Tuomisto 2012). The Hill function used in this study differs from that of our previous papers that was based on either minimum distances among species (Scheiner 2012) or mean interspecific distances (Presley, Scheiner & Willig 2014). In using all pairwise distances to compute Hill diversity, our new formulation reflects comprehensive information about variability that was not captured in our earlier metrics.

Finally, we combine functional-trait species diversity and mean dispersion into an integrated metric, functional-trait dispersion:

$${}^qD(TM) = 1 + {}^qD(T) \times M, \quad \text{eqn 5}$$

or equivalently as:

$${}^qD(TM) = 1 + (S - 1) \times {}^qE(T) \times M', \quad \text{eqn 6}$$

where $M' = \frac{S}{S-1}M$, range $[0, 1]$. Equation 6 emphasizes that the metric combines species richness, functional-trait evenness and mean dispersion (see the Appendix S1 for a proof of the equality of the two formulations). We call this metric ‘functional-trait dispersion’ because it is determined by the dispersion of species in trait space and measures the effective number of functionally distinct species; it has a range of $[1, S]$. We represent the new metric as ${}^qD(TM)$ to emphasize that it combines Hill diversity based on functional traits (T) and mean distance (M). When all species are equally distant from each other, ${}^qE(T) = 1$, but also $M' = 1$ because distances are standardized, so that ${}^qD(TM) = S$. As the evenness of the dispersion decreases, both ${}^qE(T)$ and M' will decrease, with the exact changes in that dispersion determining how each component is affected. Thus, the ‘effective number’ of species can be thought of as the proportional decrease from actual species richness due to deviations from a perfectly equitable dispersion of species. This metric also allows functional information to be combined with abundance information through equivalent versions of M , ${}^qD(T)$, ${}^qE(T)$ and ${}^qD(TM)$ (Table S1, see Appendix S1 for derivations). When abundance is included, the effective number also includes a component due to deviations from a perfectly even number of individuals in each species. An R-script for computing all of these metrics was written by Shan Kothari, University of Minnesota, and is available on Github at: <https://github.com/ShanKothari/DecomposingFD>.

WHOLE-PART RELATIONSHIPS

A limitation of most other metrics of functional diversity is that approaches for decomposing them within and among subgroups remain unclear. By convention, we refer to the diversity of the entire set (e.g. landscape) as γ -diversity, the mean diversity within subgroups (e.g. communities) as α -diversity and the variation among subgroups as β -diversity. Here, we use a spatial structure, referring to the entire set as the landscape and the subgroups as communities. Most often such whole-part relationships refer to spatial subgroups, but need not. For example we might be interested in the relationship of a set of species into predefined groups or a clade into subclades. We also make a distinction between unstructured γ -diversity – the diversity of the entire set considered as a single unit without reference to part affiliation – as compared to structured γ -diversity – the diversity of the entire set when part affiliation is integral to the concept and its measurement (see also Kosman 2014).

For our dispersion metric (M), the whole-part is an additive relationship: $M_\gamma = M_\alpha + M_\beta$ (see eqs. A26, A30 and A32 in Appendix S1). For Hill diversity, a common relationship is multiplicative. For abundance data, ${}^qD(A)_\gamma = {}^qD(A)_\alpha \times {}^qD(A)_\beta$, although disagreements exist as to how ${}^qD_\alpha$ should be computed (Jost 2007; Tuomisto 2010). For such a relationship, β -diversity is the effective number of communities that would each contain a unique set of equally abundant species and is usually computed from the ratio: ${}^qD(A)_\gamma / {}^qD(A)_\alpha$. For our treatment of functional data, however, this multiplicative partition should not be used because it does not properly account for within- and among-community variation. Instead, ${}^qD(T)_\beta$ is calculated by first computing the distances between each pair of communities (eq. A29) and then applying eqs. 3 and 4 (eqs. A34 and A4), resulting in a measure of the effective number of equally distant communities. Defined in this way, there is no simple mathematical relationship between γ -, α - and β -diversities.

Because ${}^qD(T)_\beta$ reaches its maximum value when communities are equally distant, it does not distinguish between communities that are close from those that are distant. To provide such discrimination, functional-trait species diversity must be combined with mean dispersion. It is not possible to compute ${}^qD(TM)_\beta$ directly from ${}^qD(TM)_\gamma$ and ${}^qD(TM)_\alpha$ because its components [M_γ and ${}^qD(T)_\gamma$] have different partitions – additive and multiplicative respectively – so that performing either partition alone is open to question. Instead, ${}^qD(TM)_\beta$ is computed by calculating M_β and ${}^qD(T)_\beta$, and applying eq. 2 (eq. A40). ${}^qD(TM)_\beta$ provides a measure of the effective number of functionally distinct communities. As with unstructured γ -diversity, for structured γ -diversity, α -diversity and β -diversity, abundance information can be incorporated using appropriately modified versions of eqs. A22–A25.

Constructed data

UNSTRUCTURED γ -DIVERSITY

We illustrate the behaviour of ${}^qD(TM)$ and compare it to that of other metrics through the use of constructed and empirical

data sets. The constructed data sets are simple and designed to manipulate the distribution of trait values among and within communities so as to demonstrate the behaviour of the metric with respect to distinctive types of variation in functional traits (Fig. 2). The empirical data demonstrate how the metrics behave when confronted with the complexities of ecological reality.

For the constructed data sets, we considered the traits to be measured on a ratio scale and measured distance as mean character difference, also known as weighted Manhattan distance. Based on the criteria for a metric of functional diversity that we listed in the Introduction, functional-trait dispersion, ${}^qD(TM)$, behaves as desired (Table 1). Compared to Landscape 1, Landscapes 2 and 4 each have greater functional diversity. Landscape 2 has greater functional diversity because it contains more species within the same total volume, whereas Landscape 4 has greater functional diversity because it comprises species that are more dispersed in trait space (albeit with the same species richness). Conversely, Landscapes 3, 5 and 6 are less diverse than Landscape 1 because their species are either closer together within the same total dispersion (i.e. Landscape 3), or less dispersed overall and contain fewer species (i.e. Landscapes 5 and 6). In general, ${}^qD(TM)$ captures these notions of diversity, whereas ${}^qD(T)$ and M , indicate which components of the integrated metric are responsible for those differences (Tables 1 and S2). For example Landscape 2 has a lower mean distance among species than does Landscape 1, whereas the functional-trait species diversity [${}^1D(T)$] of Landscape 3 is only slightly greater than that of Landscape 1, reflecting a similar functional-trait evenness.

We compared our metric with other commonly used diversity metrics calculated using R (R Core Team 2015). FD was calculated using the 'treedive' function from the vegan library (Oksanen *et al.* 2015). FAD was calculated as the sum of all pairwise distances (mean character differences) using the 'dist' function. FRic, FEve, FDis and FDiv were calculated using the FD package (Laliberté, Legendre & Shipley 2014). For metrics that involved abundances, we assumed that all species were equally abundant, thereby isolating effects of changes in functional diversity rather than confounding changes in abundance and function. Because ${}^qFD(Q) = FAD$ and $Q = M$ when all species have equal abundances, we did not include those metrics in our analyses.

None of the other metrics behave in a manner that corresponds to our criteria for an effective metric of functional diversity based on the uniqueness concept. For metrics involving branch lengths – FD and FEve – Landscape 4 has the lowest values. The largest value for FD occurs for Landscape 3, reflecting that metric's emphasis on evenness of minimum distances. The largest value for FEve occurs for Landscape 6, because the metric imposes a penalty against high species richness. For one of the metrics involving convex hulls, FRic identifies Landscape 5 as the most diverse and it fails to distinguish between Landscapes 1 and 2. For FDiv, the smallest value occurs for Landscape 2, again reflecting that metric's emphasis on evenness of minimum distances. Of the metrics based on distances, FDis and FDiv recognize Landscape 4 as the most diverse, but identify Landscape 2 as the least diverse. In contrast, FAD indicates that Landscape 2 is substantially more diverse than the others because the metric fails to account for species richness.

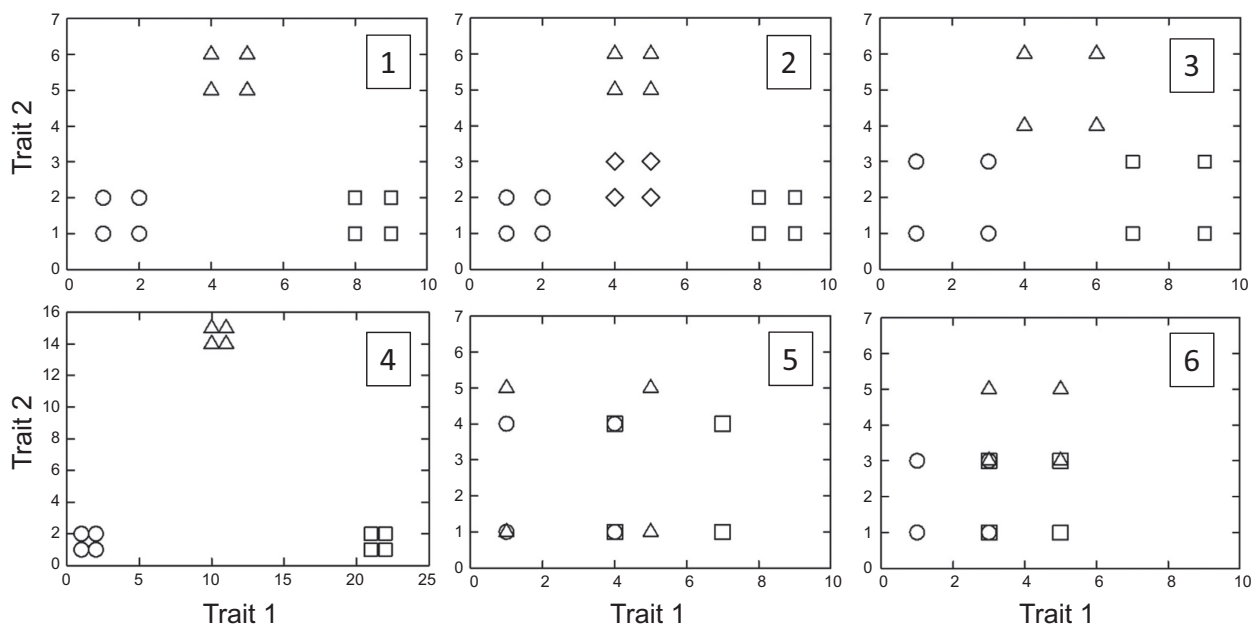


Fig. 2. Graphic representation of species in functional space defined by two traits for multiple communities within a landscape. Each landscape (numbered 1–6) contains three or four communities that each comprise four species. Within a landscape, species designated by the same shape belong to the same community. Superimposed shapes indicate that the same species is a member of more than one community. The axis ranges are the same for all landscapes, except landscape 4.

Table 1. Species richness and values of functional diversity metrics (Table S1) for constructed and empirical data sets

Data set	S	FD	FAD	FRic	FEve	FDIs	FDiv	${}^1D(T)$	M	${}^1E(T)$	M'	${}^1D(TM)$
Constructed data												
Landscape 1	12	5.33	50.89	0.48	0.65	0.45	0.88	11.12	0.35	0.93	0.38	4.89
Landscape 2	16	6.61	78.67	0.48	0.82	0.37	0.73	14.91	0.31	0.93	0.33	5.62
Landscape 3	12	7.00	46.67	0.57	0.90	0.39	0.75	11.42	0.32	0.95	0.35	4.65
Landscape 4	12	4.59	58.70	0.50	0.34	0.55	0.95	10.67	0.41	0.89	0.45	5.38
Landscape 5	9	6.80	29.37	0.66	0.80	0.46	0.82	8.54	0.36	0.95	0.41	4.07
Landscape 6	8	6.80	21.60	0.56	1.00	0.42	0.78	7.66	0.34	0.96	0.39	3.60
Empirical data												
500 m a.s.l.	76	187.83	15 626.86	1.43	0.64	1.52	0.85	72.21	0.35	0.95	0.36	26.62
750 m a.s.l.	64	160.61	10 835.73	0.83	0.64	1.49	0.83	60.45	0.35	0.94	0.35	21.88
1000 m a.s.l.	52	141.22	6919.88	2.51	0.63	1.46	0.83	49.00	0.33	0.94	0.34	17.35
1250 m a.s.l.	45	111.89	4878.07	1.83	0.60	1.41	0.81	42.09	0.32	0.94	0.32	14.26
1500 m a.s.l.	26	75.44	1587.43	2.58	0.61	1.40	0.82	24.14	0.30	0.93	0.31	8.23
1750 m a.s.l.	19	53.86	756.06	1.10	0.57	1.29	0.76	17.38	0.27	0.91	0.29	5.69
2000 m a.s.l.	15	52.52	563.00	3.34	0.69	1.46	0.83	14.03	0.32	0.94	0.35	5.54
2250 m a.s.l.	11	44.82	304.87	2.60	0.77	1.47	0.87	10.32	0.33	0.94	0.36	4.40
2500 m a.s.l.	14	51.47	510.78	3.41	0.79	1.52	0.88	13.14	0.35	0.94	0.38	5.60
2750 m a.s.l.	11	45.51	310.40	3.34	0.82	1.52	0.85	10.43	0.34	0.95	0.38	4.58
3000 m a.s.l.	8	36.42	169.42	2.79	0.78	1.56	0.93	7.61	0.34	0.95	0.39	3.59
3250 m a.s.l.	7	33.97	126.28	2.94	0.78	1.52	0.81	6.67	0.33	0.95	0.39	3.22
3500 m a.s.l.	6	32.94	87.75	3.01	0.79	1.45	0.83	5.74	0.30	0.96	0.36	2.74
All Manu	92	212.31	23 330.06	1.68	0.60	1.54	0.85	87.11	0.36	0.95	0.37	32.49

When all species have equal abundances, ${}^qD(Q) = FAD$ and $Q = M$. Numbers listed for empirical data refer to elevational strata.

S, species richness; FD, functional diversity; FAD, functional attribute diversity; FRic, functional richness; FEve, functional evenness; FDis, functional distance; FDiv, functional divergence; ${}^1D(T)$, functional-trait species diversity; M , mean dispersion; ${}^1E(T)$, functional-trait evenness; M' , standardized mean dispersion; ${}^1D(TM)$, functional-trait dispersion.

Our metrics of functional diversity capture the same information as do current metrics, but in a way that allows them to be integrated into a single metric. Species richness, mean dispersion (M) and FAD have a simple mathematical relationship (Table S1). For these constructed examples, ${}^qD(TM)$ has a rank-order correlation of 1 with FAD, with the correlation primarily being driven by the effects of species richness ($r = 0.94$, Table S2). In addition, ${}^qD(T)$ has relatively large, negative correlations with FRic, FDis and FDiv, whereas ${}^qD(TM)$ has large, negative correlations with FD, FRic and FEve. Because our constructed examples were designed to mostly explore the effect of changes in M , these comparisons do not provide a definitive assessment of how our metric compares with others. Such a comparison requires a large scale simulation like that of Mouchet *et al.* (2010). However, our comparisons suggest that many of the properties captured by those other metrics are included within ours, and that our integrated metric – ${}^qD(TM)$ – suitably represents overall functional diversity.

α - AND β -DIVERSITY

Our integrated metric captures features based on considerations of whole-part relationships (Table 2). For α -diversity in Landscapes 1, 2 and 4, the distances among the species within each community are the same. Yet, the value of ${}^qD(TM)_\alpha$ for Landscape 4 is less than that of the other landscapes because the relative distances among the species within each community are smaller than in other landscapes due to the

standardizing of distances to the span of trait values across the entire landscape. As a result, the value of M_α for Landscape 4 is substantially lower than the others. In contrast, the value of ${}^qD(T)_\alpha$ for all landscapes is about the same.

For similar reasons, ${}^qD(TM)_\beta$ captures differences in distances among the communities (e.g. Landscape 1 vs. Landscape 4). In contrast, ${}^qD(T)_\beta$ provides a better measure of the number of distinct communities with respect to species identities. We did not attempt a whole-part decomposition for the other diversity metrics because all would give patterns already reflected in M , ${}^qD(T)$ or ${}^qD(TM)$. Moreover, it is not clear that such a partition is possible for measures that involve branch lengths or convex hulls (see Discussion). As we stated previously, ${}^qD(TM)_\beta$ needs to be measured directly from the data rather than as ${}^qD(TM)_\gamma/{}^qD(TM)_\alpha$. To see why, consider Landscapes 1 through 4. In all cases, the computed ratio results in a number of effective communities that is larger than the actual number of communities (e.g. 4–8 for Landscape 4). As the effective number should always be no greater than the actual number, clearly such an operation leads to incorrect values.

For functional traits, because unstructured γ -diversity and structured γ -diversity measure different landscape properties, their values need not be identical (Tables 1 and 2). Species that occur in more than one community must be treated differently when the entire landscape is considered as a single unit as compared to when the landscape is considered to be an aggregation of subunits. In the case of unstructured γ -diversity, each species is considered only once in the calculation. In the case of

Table 2. Spatial decompositions of functional diversity of the constructed and empirical data sets into landscape (structured γ), within-community (α) and among-community (β) components

Data set	S_γ	S_α	S_β	${}^1D(T)_\gamma$	${}^1D(T)_\alpha$	${}^1D(T)_\beta$	M_γ	M_α	M_β	${}^1D(TM)_\gamma$	${}^1D(TM)_\alpha$	${}^1D(TM)_\beta$
Landscape 1	12	4.00	3.00	11.12	3.88	2.99	0.35	0.07	0.28	4.89	1.27	1.84
Landscape 2	16	4.00	4.00	14.91	3.88	3.89	0.31	0.07	0.24	5.62	1.27	1.93
Landscape 3	12	4.00	3.00	11.42	3.88	3.00	0.32	0.14	0.19	4.65	1.54	1.57
Landscape 4	12	4.00	3.00	10.67	3.89	2.98	0.41	0.03	0.38	5.38	1.12	2.13
Landscape 5	9	4.00	2.25	11.15	3.89	2.91	0.34	0.29	0.06	4.79	2.13	1.17
Landscape 6	8	4.00	2.00	11.05	3.90	2.93	0.29	0.20	0.09	4.21	1.78	1.26
Manu	92	27.23	3.38	330.66	18.07	11.82	0.34	0.33	0.01	113.81	6.67	1.11

structured γ -diversity, each species in each subunit is considered as a separate entity. To see why, imagine two landscapes. The first contains species A that is found in two constituent communities along with other species (Landscape AA). The second contains species A and B, each in separate communities, with each species having identical functional attributes (Landscape AB). Because species A and B are identical from a functional perspective, the functional diversities of Landscapes AA and AB should be equal. That equality is achieved in Landscape AA only if species A in each of its constituent communities is treated as a distinct entity for the calculation of functional diversity of the entire landscape. This requirement for calculating γ -diversity differently in unstructured and structured contexts holds for all other metrics of functional diversity (Table S1).

Empirical data

METHODS

To explore the behaviour of our metrics of functional diversity based on empirical data, we focused on the bat fauna of the Manu Biosphere Reserve (hereafter Manu, Patterson, Stotz & Solari 2006). This reserve is located on the eastern slopes of the Andes in southeastern Peru (MacQuarrie 1992). It spans an extensive elevational range (340 to 3625 m a.s.l.) and supports structurally and compositionally distinct vegetation types that occur sequentially along the elevational gradient (Terborgh 1971; Patterson *et al.* 1998). Vegetation varies from lowland rain forest (<500 m a.s.l.) with 50 to 60 m canopies, to patches of elfin forest (>3200 m a.s.l.) characterized by a low canopy (3–5 m) and dense vegetation intermixed with tall grasslands.

The elevational distributions of the bat species are based on comprehensive surveys conducted over many years (Table S2, Patterson, Stotz & Solari 2006). Data on species incidence were organized into thirteen 250 m elevational strata, with each stratum denoted as a community for our analyses. The strata were chosen to balance the resolution of empirical records and the amount of collection effort in each interval (Presley *et al.* 2012).

Functional diversity was characterized using 16 categorical and 10 continuous traits that were separated into six groups: diet, foraging location, foraging strategy, body size, masticatory mode and flight ability (Table S3, Cisneros *et al.* 2014). Categorical traits were binary (i.e. a species did or did not exhibit a trait) and characterized species

diet (fruit, nectar, invertebrates, vertebrates, fish, blood), foraging location (open areas, over water, above canopy, canopy, subcanopy, understory) or foraging strategy (aerial, gleaning, hovering, other). Continuous traits characterized body size (mass, forearm length), masticatory mode (greatest length of skull, condylobasal length, maxillary tooth row length, breadth across upper molars, post-orbital constriction, breadth of braincase) and flight ability (wing aspect ratio, wing loading), which reflect physiological constraints, diet and foraging behaviour respectively. To ensure that skull measurements associated with masticatory mode represented more than variation in body size, principle component analysis was performed with varimax rotation. The first two principal components, which together accounted for 90% of the variation in skull attributes and represented variation in skull size and skull shape, respectively, were used in subsequent analyses. To determine the functional distance between each bat species, Jaccard dissimilarity was calculated for each group of binary traits and the mean character difference was calculated for each group of continuous traits. Then the combined distance (d_{ij}) between species was determined by an equal-weight averaging of the six group-specific distances; we confirmed that the corresponding distances between communities (d_{mAB} , eq. A29) were non-negative and contained within the interval [0,1].

α -, β - AND γ -DIVERSITY

We first consider the unstructured γ -diversity of bats along the entire elevational gradient (Table 1, All Manu). A total of 92 species of bats occurred along the elevational gradient, with species richness decreasing from 76 species at 500 m to six species at 3500 m (Cisneros *et al.* 2014). The distribution of species ranges along that gradient was primarily nested (Table S3), exhibiting clumped species-loss with increasing elevation (Presley *et al.* 2012). Rare species – those present in only one or two sites – were found almost exclusively at low elevations, although a few species were found only at mid- or high elevations. The standardized mean dispersion ($M' = 0.37$) of the entire landscape indicates substantial clumping in trait space, mostly within guilds (Fig. 3), whereas the evenness of dispersion [${}^1E(T) = 0.95$] indicates that the effective number of functionally distinct species, ${}^1D(T)$, is close to the maximum (S). The estimate of functional-trait dispersion for the

landscape [${}^1D(TM) = 32.49$] indicates that although the species are distinct from a functional perspective, they still cluster into groups that reflect our notion of the number of functional types at Manu. Neotropical bats have been categorized into ten functional groups or guilds (Kalko 1997) based on: (1) the density of vegetation through which they fly, which is related to foraging location and flight ability in our classification, (2) foraging mode, which is comparable to foraging strategy in our classification and (3) diet, which is comparable to diet and masticatory mode in our classification. Of those, eight guilds are present at Manu: aerial insectivores, high-flying insectivores, gleaning omnivores, canopy frugivores, understory frugivores, nectarivores, sanguinivores and piscivores. In addition to criteria used by Kalko (1997), we include body size to distinguish additional aspects of species niches. Indeed, body size differs among species within functional groups as well as between functional groups. Consequently, an estimate of an effective number of functionally distinct species of approximately 32 types of bats at Manu is plausible given the number of functional groups and the size variation within the fauna.

Across the elevational gradient, the correlation of species richness with ${}^1E(T)$ was weakly negative ($r = -0.49$) and with M' more strongly negative ($r = -0.62$; Table S5). M' and ${}^1E(T)$ were positively correlated with each other ($r = 0.77$), indicating that mean dispersion and the evenness of dispersion were closely linked despite considerable variation in the composition and richness of elevationally defined communities (Fig. S1). Importantly, this was not true for the artificially constructed data sets ($r = -0.12$), illustrating that the metrics are not confounded mathematically. In contrast, ${}^1D(T)$ and ${}^1D(TM)$ were each highly correlated with species richness ($r = 0.99$ and 1.00 respectively).

With respect to elevation, mean dispersion (M') increased significantly ($r = 0.64$), evenness [${}^1E(T)$] increased but not significantly ($r = 0.51$) and species richness, ${}^1D(T)$ and ${}^1D(TM)$ decreased significantly ($r = -0.99$, $r = -0.98$ and $r = -0.96$, respectively, Fig. 4). Variation in species richness played the dominant role in moulding the gradient of functional-trait dispersion [${}^1D(T)$]. The elevational decrease in species richness and the associated nested structure of species distributions are attributable to both the loss of rare functional groups with increasing elevation and a decrease in diversity within those

groups (Table S3, Fig. S1). Only four of the eight functional groups (i.e. aerial insectivores, canopy frugivores, understory frugivores and nectarivores) span the entire elevational gradient. Despite relatively small variation in the evenness of dispersion [${}^1E(T)$ ranged from 0.91 to 0.95] and mean dispersion (M' ranged from 0.31 to 0.39), each of these metrics were somewhat lower at mid-elevations than at low or high elevations. The initial decline in M' was associated with losses of species from higher trophic levels. More specifically, all species of piscivores, sanguinivores and high-flying insectivores, and all but one species of gleaning omnivore were not present at or above 1500 m (Fig. S1). Greater mean dispersion characterized strata from 1750 to 2000 m due to the loss of frugivorous species and the addition of an aerial insectivore. At higher elevations, species were lost in more-or-less similar proportions from each of the remaining functional groups, resulting in little change in M' throughout most of that part of the gradient.

The loss of species and functional groups with increasing elevation is associated with changes in the diversity and abundance of resources on which bats feed as well as with the thermal environment. Resources are most abundant and diverse in lowland rain forest (below 600 m). As temperature and the abundances of each resource type decline with elevation, fewer populations can be sustained, with only species that are smaller or better able to thermoregulate persisting at the upper elevations (Cisneros *et al.* 2014). The relative invariance of M' indicates that the mean distance between functional types and the relative proportion of species belonging to each functional type are essentially constant along the gradient. Taken together, this suggests that general rules based on limiting similarity of bats may be guiding species assembly along elevational gradients of temperature and productivity.

The relatively low value (6.67) for ${}^1D(TM)_\alpha$ results from the uneven representation of functional types and the paucity of functional types along most of the gradient (Fig. S1). In contrast, mean within-site dispersion ($M_\alpha = 0.33$) was nearly equal to that for the entire gradient ($M_\gamma = 0.34$), indicating that mean dispersion of species in trait space varied little along the gradient. The M_β of 0.01 and ${}^1D(TM)_\beta$ of 1.11 indicate that functional differences among sites were small and that functionally distinct communities do not occur along the gradient. Both of these phenomena reflect the nested structure of

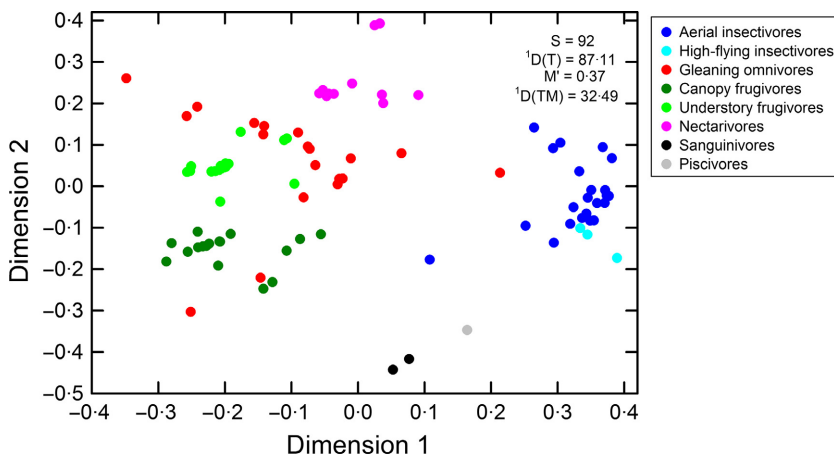


Fig. 3. The distribution of the 92 bat species from the elevational gradient at Manu with respect to the first two trait-space axes as determined by NMDS. The axes account for 70% and 20% of the variation, respectively.

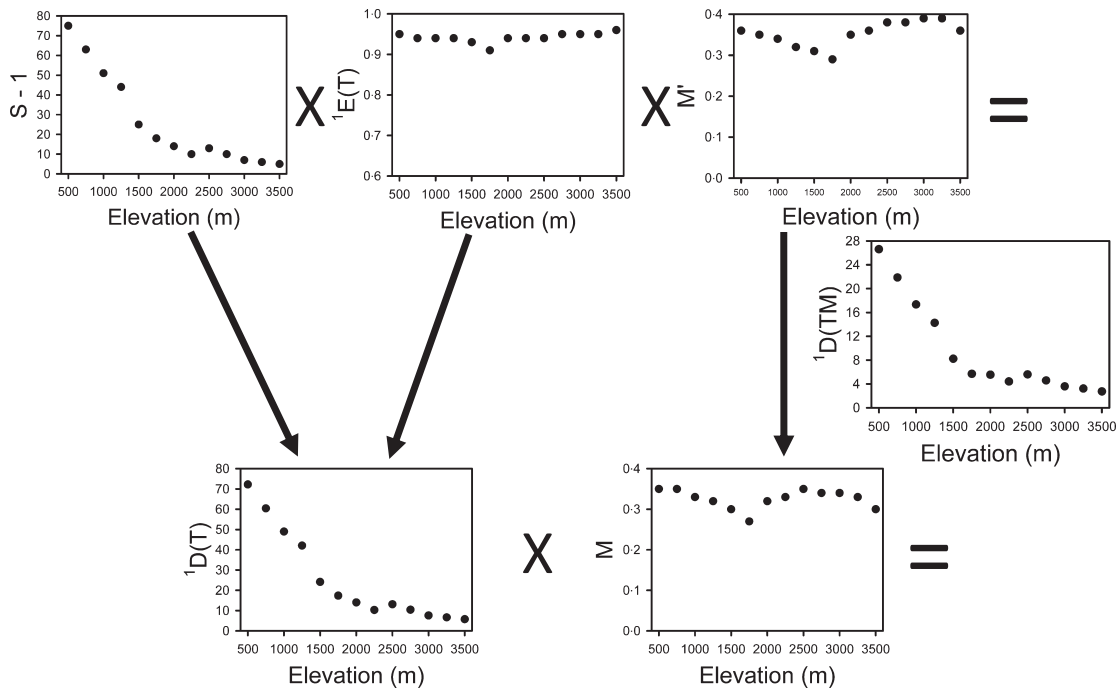


Fig. 4. Elevational gradients in metrics of functional diversity. The upper graphs represent components of Equation 6 [$S-1$, ${}^1E(T)$ and M'], whereas the lower graphs represent components of Equation 5 [${}^1D(T)$ and M]. The graph to the far right [${}^1D(TM)$] is a consequence of the product of the elevational patterns for $S-1$, ${}^1E(T)$, and M' or the product of the elevational patterns for ${}^1D(T)$ and M . The arrows indicate conceptual linkages between the components of the two equations.

communities such that functional types occurring at functionally poor elevations also occur at more functionally rich elevations.

Consideration of functional-trait dispersion [${}^1D(TM)$], as well as its components and partitions, facilitates the interpretation of complex patterns in the elevational gradient of bat functional variability. Other commonly used functional metrics do not expand our interpretive ability. FD and FAD each had rank correlations of 1.0 with ${}^1D(T)$ and 0.99 with ${}^1D(TM)$, and FRic and FEve each had large, negative correlations with both (c. -0.7 , Table S5). For M' , all of the other metrics had large correlations (c. 0.6–0.9), either positive (FRic, FEve, FDis and FDiv) or negative (FD and FAD). Consequently, our metric and its components enable a comprehensive analysis and interpretation of functional-trait dispersion, with explicit recognition of how variation in functional-trait dispersion is driven by variation in species richness, in the effective number of functionally distinct species and in mean dispersion (Fig. 4).

Discussion

DECOMPOSING AND COMPARING BIODIVERSITY

Despite its broad use in the ecological and conservation literature, and its somewhat intuitive appearance, biodiversity is a complex concept. Any metric of biodiversity is likely to encompass multiple components and measure a variety of attributes. ${}^qD(TM)$ is one such metric. We demonstrated that ${}^qD(TM)$ comports to desirable criteria for a metric of functional diversity and that it can be decomposed in a variety of ways that

facilitate the understanding of patterns of variation. First, the metric has components of dispersion, evenness and species richness that can be examined separately or in combination, including a measure of the effective number of functionally distinct species. For example the bats at Manu are functionally distinct based on values of ${}^qD(T)$ close to S , but overall diversity [${}^qD(TM)$] indicates that taxa can be grouped into a smaller number of functional subsets. Second, we can decompose our metric in a hierarchical fashion (i.e. α - and β -diversity). Other metrics do not possess this flexibility.

We showed that variation in other metrics of functional diversity is significantly associated with variation in our measures of dispersion and evenness. However, comparisons of those metrics with measures of diversity based on other characteristics such as abundance or phylogeny are hampered because they are measuring different properties. ${}^qD(TM)$ is based on quantities of distance and the effective number of functionally distinct species. The latter aspect facilitates comparisons with abundance diversity and phylogenetic diversity when they are also measured as effective numbers (Scheiner 2012).

Most functional diversity metrics cannot be decomposed into α - and β -components. The exceptions are FAD which can be additively partitioned because it is based on the sum of distances, Rao's Q which can similarly be additively partitioned or multiplicatively partitioned given suitable transformation (De Bello *et al.* 2010; Pavoine, Marcon & Ricotta 2016), and ${}^qFD(Q)$ which can be multiplicatively partitioned (Chiu & Chao 2014). Partitioning FRic has the same limitations as does the metric itself. An additive partition of that metric is feasible. However, for Landscapes 1 and 2, the mean hull volumes of

the communities, α -diversity, would be the same, so that the two landscapes would have the same β -diversities. That result contradicts intuition concerning the relative β -diversities of the two landscapes. A similar problem arises with partitioning FDiv, with the added complication of its use of centroids. For the metrics that are based on dendrograms (FD and FEve), all values must be rooted to the same locations or otherwise use the same dendrogram for each part and for the whole. Critically, the ecological meaning of branch length sums for such parts remains unclear. For each of these metrics, the ecological meaning of β -diversity needs to be explicated. For metrics involving Hill diversity – ${}^qD(T)$, ${}^qD(TM)$ and ${}^qFD(Q)$ – β -diversity is the effective number of functionally distinct communities. As with the effective number of species, such a measure is comparable across systems even if based on completely different traits or if based on other species attributes such as abundance or position in a phylogeny.

USING DIVERSITY METRICS

The choice of an appropriate metric of functional diversity depends on the scientific question of interest. Nonetheless, nearly all of the efforts related to these metrics has been devoted to metric development. Future research should shift that focus to more intimately consider the link between metrics and ecological or evolutionary processes and theories. Indeed, ecological and evolutionary processes can have a variety of effects on functional diversity. If communities are structured by competition through niche partitioning that limits functional similarity, then overdispersion of species in functional space should characterize communities compared to the functional dispersion of the same number of species randomly drawn from a regional species pool (Connell 1980). In evolutionary time, we might see the appearance of character displacement. In contrast, functional underdispersion is consistent with environmental filtering associated with physiological tolerances, habitat affinities or resource requirements shared by the species that inhabit a site (Cavender-Bares *et al.* 2009). For example the high evenness values and low β -diversity values of bats at Manu are consistent with limiting similarity operating within communities. Further insight into these processes can be gained by comparing patterns of functional diversity with those of phylogenetic and abundance diversity (Kluge & Kessler 2011). Being able to express all of these types of diversity as the effective number of species facilitates such comparisons.

Most of the common metrics of functional diversity also weight species identity with abundance. As such, they assume that the effects of abundance are linear and equal for all species and all traits. In addition, they require that abundance data to be available and accurate, which is often not the case when information is assembled from the literature to address questions about patterns of functional diversity across regional to global scales. For analyses at regional or larger extents, it remains unclear how abundance information should be aggregated from local communities, even if it is available. More importantly, not all questions concerning functional diversity involve abundance. For example some questions regarding the

evolution of niche differentiation or the filtering of regional species pools, are not likely to operate through per capita effects so that weighting by abundance would be inappropriate. Combining abundance and functional information into a joint measure of diversity is most appropriate when the assumed mechanisms of action are based on per capita effects, such as density-dependent predation or competition. Even then, the incorporation assumes that abundance effects are linear and that abundance values have equal functional consequences for all species. For example total biomass might be a better weighting factor for questions involving resource consumption or energy use (Vance-Chalcraft *et al.* 2010). Finally, population abundances are transient and may not be informative for long-term processes such as co-evolutionary interactions. Thus, combining abundance and functional information should be done with caution and only when the mechanisms being explored involve per capita processes.

Each scientific question or theory test should be explored in the context of an appropriate conceptual framework. The two functional diversity concepts described in the Introduction – the uniqueness concept and the combinatorics concept – are appropriate for different questions. For example the uniqueness concept and the associated diversity metrics presented in this paper might be more appropriate for questions involving the evolution of niche differentiation because functional-trait dispersion is maximized when the species are as functionally different as possible. In contrast, the combinatorics concept might be more appropriate for questions about food web structure because functional diversity is maximized when the community contains as many combinations of trophic links as possible.

Conservation and management efforts typically have three interrelated goals, the preservation of biodiversity for its own sake, the maintenance of ecosystem processes, or the preservation or enhancement of ecosystem services. The second and third goals require an understanding of the relationship of function-of diversity or function-for diversity with ecosystem processes. Such understanding is enhanced by approaches in which ecosystem properties are considered as functions of species properties (Scheiner 2012), thereby facilitating an assessment of the particular metrics of functional diversity that represent adequate proxies for particular ecosystem properties.

For the preservation of biodiversity, metrics of the effective number of species may be the most useful. Most preservation efforts focus on species richness, also a measure of the number of species. Similarly, phylogenetic diversity can be expressed in effective numbers. The use of related properties makes it easier to compare how a specific conservation or management strategy would differentially affect multiple aspects of biodiversity.

Conclusion

Many issues remain to be resolved with respect to the concepts of functional diversity and the metrics that characterize it. Relevant for all metrics are issues concerning the selection of functional traits and the algorithms for estimating inter-specific distances in functional space. In addition, trait values are typically correlated across species (e.g. size-related traits).

Neither our metric, nor any of the other metrics of functional diversity, account for such character correlations. Doing so requires alternative approaches to measuring dispersion-within and distances between communities (Kosman 1996, 2014; Kosman & Leonard 2007).

For the most part, each species is considered to be functionally uniform, yet we know that individuals within species vary. Such variation may be systematic (e.g. related to sex, life stages or developmental niche shifts), environmentally induced (e.g. phenotypic plasticity, developmental accommodation) or random, and it can affect the ecological range of a species. Just as diversity can be partitioned within and among communities in a landscape, it can also be partitioned among individuals within a species. A generalist species can consist of individuals with similar characteristics that enable high fitness in many environments, or can consist of individuals that differ in their characteristics, each with high fitness in different environments. Exploring how these different types of generalists relate to functional diversity of entire communities requires a diversity metric that can incorporate individual variation (eqs. A15–21).

Above all, further development of diversity metrics should be tied to ecological and evolutionary theory so that the metrics can inform deeper understanding and be useful for management. The multifaceted nature of diversity requires metrics that capture a range of characteristics, both as an integrated metric and as separate components. The metric presented in this paper is a step in that direction.

Authors' contributions

All authors contributed to the development of the ideas and the writing of the manuscript. The analytical theory was developed by E.K. The data were compiled by S.J.P. and M.R.W. and analysed by E.K., S.P. and S.M.S.

Acknowledgements

This work was facilitated by participation of S.J.P. and M.R.W., in a project entitled 'The Dimensions of Biodiversity Distributed Graduate Seminar', which was funded by a U.S. National Science Foundation grant to S. Andelman and J. Parish (DEB-1050680). S.J.P. and M.R.W. also were supported by the U.S. National Science Foundation (DEB-1239764) and by the Center for Environmental Sciences and Engineering at the University of Connecticut. The collaboration between E.K. and S.M.S., S.J.P. and M.R.W. was initiated due to support of the Colton Foundation at Tel Aviv University. This manuscript is based on work done by S.M.S. while serving at the U.S. National Science Foundation. The views expressed in this paper do not necessarily reflect those of the U.S. National Science Foundation or the United States Government.

Data accessibility

Bat trait data and species distributions across communities: uploaded as online supporting material

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Received 8 May 2016; accepted 23 October 2016

Handling Editor: Anne Chao

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1. The distribution of bat species at each elevation at Manu Biosphere Reserve with regard to the first two trait space axes as determined by a NMDS analysis of all 92 species.

Table S1. Metrics of functional diversity.

Table S2. Spearman rank correlations between functional diversity measures for the constructed landscapes.

Table S3. Incidence matrix for bats from Manu Biosphere Reserve, arranged so that species with similar spatial distributions are adjacent.

Table S4. Functional data for bats from Manu Biosphere Reserve.

Table S5. Spearman rank correlations (above the diagonal, P-values below the diagonal) between functional diversity measures as well as elevation for bats from Manu Biosphere Reserve, Peru.

Appendix S1. Detailed derivations of each metric, including abundance-based versions.