Proposing a resolution to debates on diversity partitioning

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Abstract. There have been intense debates about the decomposition of regional diversity (gamma) into its within-community component (alpha) and between-community component (beta). Although a recent *Ecology* Forum achieved consensus in the use of "numbers equivalents" (Hill numbers) as the proper choice of diversity measure, three related major issues were still left unresolved. (1) What is the precise meaning of the "independence" or "statistical independence" of alpha diversity and beta diversity? (2) Which partitioning (additive vs. multiplicative) should be used for a given application? (3) What is the proper formula for alpha diversity, as there are two formulas in the literature? This paper proposes a possible resolution to each of these issues. For the first issue, we clarify the definitions of "independence" and "statistical independence" from two perspectives so that confusion about this issue can be cleared up. We also discuss the causes of dependence, so that the dependence relationship between any two diversity components in both partitioning schemes can be rigorously justified by theory and also intuitively understood by simulation. For the second issue, both multiplicative and additive beta diversities based on Hill numbers are useful measures and quantify different aspects of communities. However, neither can be directly applied to compare relative compositional similarity or differentiation across multiple regions with different numbers of communities because multiplicative beta diversity depends on the number of communities, and additive beta diversity additionally depends on alpha (equivalently, on gamma). Such dependences should be removed. We propose transformations to remove these dependences, and we show that the transformed multiplicative beta and additive beta both lead to the same classes of measures, which are always in a range of [0, 1] and thus can be used to compare relative similarity or differentiation among communities across multiple regions. These similarity measures include multiple-community generalizations of the Sørenson, Jaccard, Horn, and Morisita-Horn measures. For the third issue, we present some observations including a finding about which alpha formula produces independent alpha and beta components. These may help to resolve the choice of a proper formula for alpha diversity. Some related issues are also briefly discussed.

Key words: *additive partitioning; alpha diversity; beta diversity; differentiation; gamma diversity; Hill numbers; multiplicative partitioning; similarity.*

Introduction

A recent Forum in *Ecology* (Ellison [2010] and papers following it) has provided an excellent updated overview of approaches to decomposing diversity. The diversity of an extended region (the gamma diversity) can be partitioned or decomposed into within- and between-community components, the alpha and beta diversities, respectively. Alpha diversity is a mean (not necessarily the arithmetic mean) of the diversities of a set of communities, whereas gamma diversity is the diversity of the pooled communities. Beta diversity is then obtained from alpha and gamma diversities based on either multiplicative or additive decomposition. There are other definitions or concepts of "beta diversity"; see Legendre and Legendre (1998), Vellend (2001), Jurasinski et al. (2009), Gregorius (2010), Tuomisto (2010),

Anderson et al. (2011), Jost et al. (2011) and Magurran and McGill (2011) for reviews and further references. Also see Moreno and Rodríguez (2010) for discussions on a consistent terminology about "beta diversity" and related topics. This paper mainly focuses on the debates about the fundamental concepts and theory of diversity partitioning.

The Forum has helped to clarify some important concepts and also has generated and stimulated fruitful discussions. Surprisingly, there was complete agreement on what had once been the most controversial point: how to quantify biological diversity. Ellison (2010:1962) summed up the Forum opinions on this point: "All of the authors in this Forum agree that using numbers equivalents instead of the classical diversity indices (entropies) ... should be used in any diversity partitioning. One could go further and suggest that, even if the interest is only in describing the diversity of a single assemblage, the numbers equivalent, not the entropy, should be the diversity measure of choice. But my goal in organizing this Forum was to move beyond this easy

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point of agreement . . . ." However, there are three related major controversial issues still left unresolved that deserve further investigation. (1) What is the precise meaning of the "independence" or "statistical independence" of alpha diversity and beta diversity? (2) Which partitioning (additive vs. multiplicative) of Hill numbers should be used in a given application? (3) What is the proper formula for alpha diversity based on Hill numbers? This paper proposes a possible resolution to each of these issues.

For the first issue, we clarify the meaning of "independence" from two different perspectives. The proposed views permit the dependence relationship between alpha and beta in both partitioning schemes to be visualized more transparently and explained more intuitively.

We discuss the second issue because Ellison (2010:1963) indicated "reaching consensus on how to partition diversity measures will be harder than agreeing on the measures themselves." As long as diversity is based on Hill numbers, both multiplicative and additive decompositions produce useful and interpretable beta components. The multiplicative and additive beta components quantify different aspects of communities and answer different questions. The controversial point involved in this issue here is: can both additive beta and multiplicative beta be used for assessing differentiation or similarity among communities, which is the goal for most diversity partitioning analysis? To compare multiple regions with different numbers of communities, we show that neither can be directly applied to measure relative compositional similarity (i.e., resemblance of species' relative abundances, species by species) or differentiation. Proper normalization is needed for each beta component. We prove that both partitioning schemes lead to the same classes of relative compositional similarity or differentiation measures.

In measuring regional heterogeneity, communities are often weighted by their areas or sizes. When community weights are considered, there are two proposed formulas for alpha diversity, first developed by Routledge (1979) and Jost (2007), respectively. This difference of opinion is the third point of contention we discuss here. We present some observations including a finding about which alpha formula produces independent alpha and beta components. These may help to resolve the choice of a proper formula for alpha diversity. Some related issues are also briefly discussed.

DIVERSITY DECOMPOSITION

Three diversity components

As we have just mentioned, there is now a consensus among Forum participants that Hill numbers (Hill 1973), including species richness, exponential of Shannon entropy, and the inverse Simpson concentration should be used instead of conventional complexity measures (such as Shannon entropy itself or the Gini-Simpson index). Therefore, our discussion will be focused on the *multiplicative and additive decompositions based on Hill numbers*. For diversity (D) calculations, assume that there are S species, and p_i denotes the relative abundance of the ith species. Hill numbers of order q, or "effective number of species," are defined for $q \neq 1$ as

$$^qD = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)}.$$ (1)

We restrict ourselves to the cases $q \geq 0$ because Hill numbers with $q < 0$ place so much weight on rare species and have poor sampling properties. The Hill number is undefined for $q = 1$, but its limit as q tends to 1 exists and gives

$$^1D = \lim_{q \to 1} {}^qD = \exp\left(-\sum_{i=1}^{S} p_i \log p_i \right).$$ (2)

The parameter q determines the sensitivity of the measure to the relative frequencies. When $q = 0$, the species abundances do not count at all and $^0D = S$. When $q = 1$, the species are weighed in proportion to their frequency and thus ^1D (= exponential of Shannon entropy) can be interpreted as the number of "typical species" in the community. When $q = 2$, abundant species are favored and rare species are discounted, and thus ^2D (= inverse Simpson concentration) can be interpreted as the number of "very abundant species" in the community. In general, if $^qD = x$, then the diversity of order q of this community is the same as that of a community with x equally abundant species. All Hill numbers are in units of "species." It is thus possible to plot them all on a single graph as a continuous function of the parameter q. This "diversity profile" characterizes the species–abundance distribution of a community and provides complete information about its diversity. Hill numbers have been extended to incorporate phylogenetic distance and also functional traits among species (Chao et al. 2010, Chao and Jost 2012, Leinster and Cobbold 2012). Thus, Hill numbers may provide a unified framework for measuring biodiversity.

Assume that there are N communities, and there are S species in the pooled communities. Let $p_{ij} \geq 0$ denote the relative abundance of the ith species in the jth community, $i = 1, 2, \ldots, S$, $j = 1, 2, \ldots, N$. Some of the p_{ij} may be zero (i.e., if a species does not exist in a community, then its relative abundance in that community is 0.) When community weights are set equal (the general case will be discussed later), the alpha and gamma components based on Hill numbers of order q are (Routledge 1979, Jost 2006, 2007):

$$^qD_\alpha = \left(\frac{1}{N}\sum_{i=1}^{S} p_{i1}^q + \frac{1}{N}\sum_{i=1}^{S} p_{i2}^q + \ldots + \frac{1}{N}\sum_{i=1}^{S} p_{iN}^q \right)^{1/(1-q)}$$
$$q \neq 1$$ (3)

and

$$^qD_\gamma = \left\{ \sum_{i=1}^{S} \left[\frac{1}{N} (p_{i1} + p_{i2} + ... + p_{iN}) \right]^q \right\}^{1/(1-q)}$$

$$q \neq 1. \qquad (4)$$

When q tends to 1, we have the following limits:

$$^1D_\alpha = \lim_{q \to 1} {}^qD_\alpha$$

$$= \exp\left(-\frac{1}{N} \sum_{i=1}^{S} p_{i1} \log p_{i1} - \frac{1}{N} \sum_{i=1}^{S} p_{i2} \log p_{i2} ... \right.$$

$$\left. -\frac{1}{N} \sum_{i=1}^{S} p_{iN} \log p_{iN} \right) \qquad (5)$$

$$^1D_\gamma = \lim_{q \to 1} {}^qD_\gamma$$

$$= \exp\left[-\sum_{i=1}^{S} \frac{1}{N} (p_{i1} + ... + p_{iN}) \log \frac{1}{N} (p_{i1} + ... \right.$$

$$\left. + p_{iN}) \right].$$

$$\qquad (6)$$

Jost (2007) proved that the partitioning of Hill numbers into independent alpha and beta (within- and between-group) components is necessarily multiplicative, as follows:

$$^qD_\beta = {}^qD_\gamma / {}^qD_\alpha. \qquad (7)$$

It takes the value of unity when all communities are identical, and it takes the value of N when all the communities are completely different from each other (no shared species). Jost (2007) interpreted multiplicative beta as "effective number of completely distinct communities." This beta measures "the extent of differentiation of communities" (Whittaker 1972). This will be discussed further in other sections.

MacArthur (1965), Lande (1996) and Veech et al. (2002) proposed instead that beta be defined through an additive relationship with alpha. This additive partitioning was meant to apply to concave measures, such as species richness, Shannon entropy, and the Gini-Simpson index. However, the latter two measures may lead to biologically inconsistent conclusions and misleading interpretations (Jost 2006, 2007, Jost et al. 2010). All authors in the Forum have agreed that diversity measures should be based on Hill numbers instead of Shannon entropy and the Gini-Simpson measure. Under an additive framework based on Hill numbers, we simply refer to the difference between gamma and alpha as "additive beta" in order to be consistent with the terminology used in the Forum. That is, additive beta is defined as follows:

$$^qD_\beta^+ = {}^qD_\gamma - {}^qD_\alpha. \qquad (8)$$

In future discussions, we would suggest that the "additive beta" be referred to as "diversity excess," and the term "beta" be limited to the between-group component of a complete partition. In the additive framework, the alpha, beta, and gamma components are all in the same units of "effective number of species." The additive beta measures "absolute differentiation" and represents the absolute magnitude of diversity "increment" or "excess" between a local scale and a regional scale. It can also be interpreted as the effective number of regional species not contained in a typical local community. Whittaker (1972) defined $^qD_\beta^+ / (^qD_\alpha)$ as "species turnover"; Jost (2007) used $^qD_\beta^+ / (N - 1)$ to measure the effective number of species unique to a typical local community. See later sections for more related measures.

A fundamental constraint

For notational simplicity, unless stated otherwise, we hereafter use (α, γ, β, β^+) for the diversities ($^qD_\alpha$, $^qD_\gamma$, $^qD_\beta$, D_β^+) defined in Eqs. 3–8. No matter which partitioning is used, if the number of communities N is fixed, then it follows from the definition of alpha and gamma diversity in Eq. 3 and Eq. 4 that for any order $q \geq 0$, (α, γ) in the positive plane satisfies the following inequality:

$$N\alpha \geq \gamma \geq \alpha \qquad (9a)$$

which is also equivalent to

$$\gamma \geq \alpha \geq \gamma/N. \qquad (9b)$$

The constraint in Eq. 9a or 9b denotes the only fundamental constraint between alpha and gamma. Here we consider $\alpha \geq 0$ in our theory as a simple starting framework. The restriction to the case $\alpha \geq L$ (including $\alpha \geq 1$, which is considered by all Forum authors) and other restrictions will be discussed later. We show later that all conclusions are valid if the condition $\alpha \geq 0$ is replaced by $\alpha \geq 1$ and $\gamma \geq N$. When $q = 2$, the constraint $N\alpha \geq \gamma$ is equivalent to $H_{GS,\gamma} - H_{GS,\alpha} \leq (1 - 1/N)(1 - H_{GS,\alpha})$ where $H_{GS,\alpha}$ and $H_{GS,\gamma}$ denote, respectively, the alpha and gamma Gini-Simpson index.

The inequality in Eq. 9a can be intuitively understood by thinking about species richness ($q = 0$), because $N\alpha$ denotes the total number of species (including repeated ones), γ denotes the species richness (excluding repeated ones) in the combined communities, and α denotes average species richness in an individual community. Similarly, a direct mathematical proof shows that the inequality is also true for "typical species" ($q = 1$) and "very abundant species" ($q = 2$), and for all $q \geq 0$.

The two beta diversities as defined in Eqs. 7 and 8 measure different aspects; thus each has its own advantages and limitations. As a simple example, if two equally large communities have no shared species, multiplicative beta gives a value of 2 for two communities having species richnesses 1 and 2, respectively. It is also 2 if the species richnesses are 100 and 200, respectively, or 100 and 2, respectively. It is a measure

of pure relative differentiation. The "magnitude" of the difference is lost in the multiplicative beta, whereas this information is kept in additive beta (the additive beta values are 1.5, 150, and 51 in these three cases). But this also shows that additive beta depends on alpha for fixed N; the additive decomposition does not produce a complete partition of regional diversity into within- and between-group components. This dependence will be discussed further.

Meaning of "Independence"

Two perspectives

One of the most contentious issues in diversity partitioning is about the meaning of "independence" or "statistical independence" of alpha and beta diversities. As Jost (2007:2428) indicated, alpha and beta measure different aspects of communities; thus they should be defined so that each is free to vary "independently" of the other. Otherwise, "if beta depends on alpha, it would be impossible to compare beta diversities of regions whose alpha diversity differed." This is the essence of a complete partitioning of any quantity into within- and between-group components; all the within-group information should be contained in one component, and all the between-group information should be contained in the other component, with no cross-talk. Jost (2007) proved that multiplicative alpha and beta defined in Eqs. 3 and 7 are "independent" in this sense.

Veech and Crist (2010a, b) commented that Jost never claimed that "independence" means "statistical independence" in his papers. They are correct; Jost was referring to a different kind of independence. First, we clarify that "*statistical* independence" refers to independence among *random variables*. All possible values that a random variable can take are characterized or controlled by a sampling scheme based on a probability distribution. To determine whether any two random variables are *statistically* independent, we must know the probability distributions of the two random variables. The authors in the Forum use two different statistical perspectives.

1. *Fixed-parameter approach (diversities are regarded as fixed parameters).*—In Jost's approach, he considered all possible values that alpha, beta, and gamma can take as fixed parameters. We call this model a fixed-parameter model. There is no sampling scheme and no probability structure involved. Therefore, as Jost indicated in his Forum paper, "*statistical* independence of alpha and beta is neither necessary nor desirable."

In Jost's approach, the "independence" of alpha and beta means that all possible values of alpha and beta are not related to each other by any systematic/mathematical constraints. That is, knowing only alpha diversity, one has no information about the value of beta diversity, and vice versa. Jost (2010:1970) further explained its meaning: "... any value in the domain of alpha is compatible with any value in the domain of beta, and vice versa" and

thus all possible values of alpha and beta form a Cartesian product of two intervals (i.e., all possible values when plotted in a two-dimensional (alpha, beta) plane form a rectangle). In statistical terms, alpha and beta are "*unrelated parameters*." In order to avoid confusion with "statistical independence," a clearer and better description of Jost's sense of "independence" is that alpha diversity and beta diversity are two "*unrelated*" parameters. When we want to prove whether alpha and beta are "unrelated," we just search whether there exist any systematic constraints between alpha and beta, as we will show. Hereafter the terminology "related" or "unrelated" ("relatedness" or "unrelatedness") always refers to fixed-parameter models.

2. *Random-parameter approach (diversities are regarded as random variables taken from a distribution).*—Focusing on species richness ($q = 0$), Veech and Crist (2010a) and Baselga (2010) regarded all possible values of alpha, beta, and gamma as *random variables* and simulated alpha and gamma randomly from a uniform distribution. We call this model a random-parameter model. In this approach, the uniform distribution is the probability structure involved in generating alpha and gamma values. Two random variables X and Y are "statistically independent" if and only if the joint distribution of X and Y is equal to the product of the two marginal distributions. This is equivalent to showing $P(X \in A, Y \in B) = P(X \in A) \times P(Y \in B)$ for any events A and B of the random variables X and Y, respectively. Veech and Crist (2010a) and Baselga (2010) used the latter criterion to show the independence of two variables in their Forum papers. For simplicity, in the following, we use "dependence" for "statistical dependence" and "independence" for "statistical independence"; these terms always refer to random-parameter models under the uniform distributions, because this is the only distribution discussed in the debates.

Independence of two random variables implies no correlation between them, but the reverse is not necessarily true. Two uncorrelated variables may not be independent. If the underlying distributions are uniform distributions, as in the simulations performed in Baselga (2010) and Veech and Crist (2010a), a nice property is that, to prove whether two uniform random variables are independent, we only need to check whether the set of all possible values that the two variables can jointly take forms a rectangle in a two-dimensional plane. If it is not a rectangle (i.e., there are systematic constraints between the two variables), then the two variables are dependent. If it is a rectangle, then the two variables are independent. Therefore, in the special case of the uniform distribution, the claim that alpha and beta are independent (dependent) in a random-parameter model is equivalent to the claim that alpha and beta are unrelated (related) if they were treated as fixed parameters. This not only bridges the two sides of debates, but also helps one to understand all

TABLE 1. Dependence induced by the fundamental constraint (A): $N\alpha \geq \gamma \geq \alpha$ under a uniform random-parameter model for fixed N and $\alpha \geq 0$ under additive vs. multiplicative partitioning.

Constraint and relationship	Additive ($\beta^+ = \gamma - \alpha$)	Multiplicative ($\beta = \gamma/\alpha$)
Constraint (A): $N\alpha \geq \gamma \geq \alpha$ for fixed N	$N\alpha \geq \gamma \geq \alpha$ (i.e., $\gamma \geq \alpha \geq \gamma/N$) $\Rightarrow$ $(N-1)\alpha \geq \beta^+$ and $(1-1/N)\gamma \geq \beta^+$	$N\alpha \geq \gamma \geq \alpha \Rightarrow N \geq \beta \geq 1$
Diversity relationship	(α, γ) dependent	(α, γ) dependent
	(α, β^+) dependent	(α, β) independent
	(β^+, γ) dependent	(β, γ) independent

Notes: The condition $\alpha \geq 0$ can be replaced by $\alpha \geq 1$ and $\gamma \geq N$. Diversities (α, γ, β, β^+) refer to Eqs. 3–8, and conclusions are valid for all $q \geq 0$. In a fixed-parameter model, replace "dependent" by "related" and replace "independent" by "unrelated." The conclusions are the same as those obtained in Baselga (2010:1980).

simulation findings about "dependence" or "relatedness" between any two diversity components discussed in the Forum. In the nonuniform case, this equivalence is no longer valid.

Theoretical approach

To theoretically determine whether any two diversity components based on Hill numbers are related in a fixed-parameter model or dependent in a random-parameter model, we only need to find whether there are systematic constraints between the two diversities due to the fundamental constraint $N\alpha \geq \gamma \geq \alpha$ given in Eq. 9a or $\gamma \geq \alpha \geq \gamma/N$ in Eq. 9b. This constraint, which is referred to as Constraint (A) for easy reference later, induces relatedness or dependence between γ and α. For the additive approach, Eq. 9a also induces the following systematic constraint between α and β^+:

$$(N-1)\alpha \geq \beta^+ \qquad (10a)$$

implying that (α, β^+) are related or dependent. Similarly, Eq. 9b also induces the following systematic constraint between γ and β^+:

$$(1 - 1/N)\gamma \geq \beta^+ \qquad (10b)$$

implying that (γ, β^+) are related or dependent. In the multiplicative approach, both Eq. 9a and Eq. 9b are equivalent to

$$N \geq \beta \geq 1. \qquad (11)$$

The upper and lower bounds for beta do not involve either alpha or gamma. Thus no constraints are induced for (α, β) or (γ, β). We now can summarize the

conclusions for a random-parameter model for $\alpha \geq 0$ in Table 1, and the same results can be obtained for $\alpha \geq 1$ and $\gamma \geq N$. The conclusions in Table 1 are valid for all orders of $q \geq 0$ and will be justified by graphical display and empirical simulation later. Because there are no other systematic constraints except for $N\alpha \geq \gamma \geq \alpha$ or $\gamma \geq \alpha \geq \gamma/N$, our approach provides a very simple theoretical justification for the dependence relationships in Table 1 for all orders of $q \geq 0$ when community weights are set equal. Our conclusions are the same as those obtained in Baselga (2010:1980).

Conditional relatedness and conditional dependence

One may wonder why there are different conclusions from those in Table 1 about "relatedness" or "dependence" reported in the Forum papers. For example, Jost (2010) concluded that multiplicative beta is related to gamma in a fixed-parameter model, Veech and Crist (2010*a*) reported in their simulations that alpha and beta are dependent in both partitioning schemes, and Baselga (2010) used simulation plots to show that the dependence relationship depends on the order of simulations. These seemingly inconsistent findings were mainly caused by *conditional* relatedness and *conditional* dependence induced by different conditions that each author imposed in their arguments or simulations. In Table 2, we list three conditions considered by the authors in the Forum. *In addition to* the dependences given in Table 1, the conditional dependence induced by each condition is given in the same table.

Condition (1): fixed alpha in a range between a lower bound L and an upper bound U.—If alpha is restricted in a range of [L, U], then this information induces a

TABLE 2. Conditional dependence for any two diversity components under a uniform random-parameter model, in addition to the dependences given in Table 1.

Condition and restriction	Additive ($\beta^+ = \gamma - \alpha$)	Multiplicative ($\beta = \gamma/\alpha$)
Condition (1) on α	$U \geq \alpha \geq L \Rightarrow U \geq \gamma - \beta^+ \geq L$	$U \geq \alpha \geq L \Rightarrow \beta \times U \geq \gamma \geq \beta \times L$
	(β^+, γ) conditionally dependent	(β, γ) conditionally dependent
Condition (1a) on α	$\alpha \geq L \Rightarrow \gamma - \beta^+ \geq L$	$\alpha \geq L \Rightarrow \gamma \geq \beta \times L$
	(β^+, γ) conditionally dependent	(β, γ) conditionally dependent
Condition (2) on γ	$U^* \geq \gamma \geq L^* \Rightarrow U^* \geq \alpha + \beta^+ \geq L^*$	$U^* \geq \gamma \geq L^* \Rightarrow U^* \geq \alpha \times \beta \geq L^*$
	(α, β^+) conditionally dependent	(α, β) conditionally dependent

Notes: The conclusions are valid for all $q \geq 0$. In a fixed-parameter model, replace "conditionally dependent" by "conditionally related." U and U^* denote upper bounds, L and L^* denote lower bounds, $U > L \geq 1$, and $U^* > L^* \geq 1$.

a) Additive partitioning ($U \geq \alpha \geq L$)

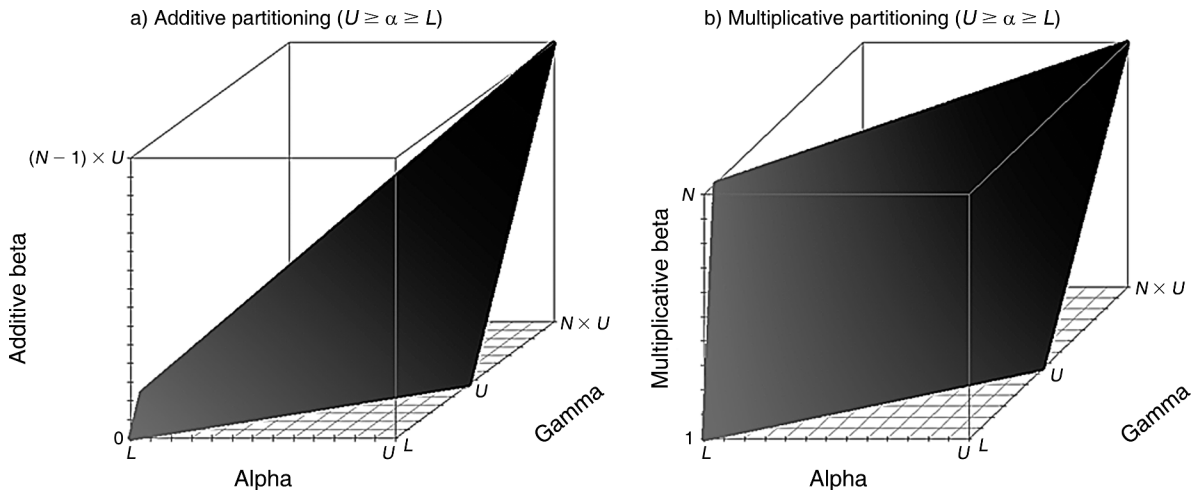b) Multiplicative partitioning ($U \geq \alpha \geq L$)

FIG. 1. Three-dimensional plot for three diversity components, where $N = 2$ (number of communities), $q = 0$ (order of Hill numbers), $L = 1$ (lower bound of alpha), and $U = 15$ (upper bound of alpha). Diversities include alpha (α), multiplicative beta (β), additive beta (β^+), and gamma (γ); see Eqs. 3–8. The surface is the same for both fixed-parameter and random-parameter models. (a) Additive partitioning with $U \geq \alpha \geq L$. The shaded area plots the surface $\{(\alpha, \beta^+, \gamma) : \gamma = \alpha + \beta^+, N\alpha \geq \gamma \geq \alpha \text{ given } U \geq \alpha \geq L\}$. None of the three two-dimensional projections is a rectangle. (b) Multiplicative partitioning with $U \geq \alpha \geq L$. The shaded area plots the surface $\{(\alpha, \beta, \gamma) : \gamma = \alpha \times \beta, N\alpha \geq \gamma \geq \alpha \text{ given } U \geq \alpha \geq L\}$. The projection onto the (α, β)-plane is a rectangle, whereas the other two-dimensional projections are not rectangles.

systematic/mathematical relationship between beta and gamma for both multiplicative and additive decompositions. Thus, beta and gamma are *conditionally* dependent in a random-parameter model (or *conditionally* related in a fixed-parameter model). Here "conditional" refers to the condition $U \geq \alpha \geq L$. Alpha and multiplicative beta remain independent under this condition on alpha because beta is independent of (or unrelated to) alpha as shown in Table 1, and no constraint on alpha affects the possible range of multiplicative beta.

Condition (1a): fixed lower bound L for alpha.—The condition $\alpha \geq L$ induces conditional relatedness or dependences between beta and gamma for both multiplicative and additive decompositions. All authors except Baselga (2010: his Procedure 1) in the Forum assumed that at least one species is found in each community. This is to impose a condition or restriction $\alpha \geq L = 1$.

Condition (2): fixed gamma in a range between a lower bound L^* and an upper bound U^*.—This information induces a systematic/mathematical relationship between alpha and beta for both multiplicative and additive betas. Thus, alpha and beta are *conditionally* dependent in a random-parameter model (or *conditionally* related in a fixed-parameter model) for both types of partitioning methods. Here "conditional" refers to the condition $U^* \geq \gamma \geq L^*$.

We first explain why these conditions in Table 2 are needed in simulations and in graphical presentation. For example, Baselga (2010) in his simulation used two procedures: Procedure 1 (fixed gamma in an interval) and Procedure 2 (fixed alpha in an interval). Without

one of the two restrictions, simulation cannot be efficiently performed and results cannot be graphically presented. Similarly, these restrictions are also needed to display the surface of (α, β, γ) or $(\alpha, \beta^+, \gamma)$ in a three-dimensional space. These displays will help one to understand dependence or relatedness between any two diversity components, as we will discuss.

Assume the set C contains all possible positive values that (α, β, γ) can take based on Hill numbers in a multiplicative partitioning. We have the following expression for C with a fundamental constraint given in Eq. 9a:

$$C = \{(\alpha, \beta, \gamma) : \gamma = \alpha \times \beta, \ N\alpha \geq \gamma \geq \alpha\}.$$

Similarly, for additive partitioning, we consider the set

$$C^+ = \{(\alpha, \beta^+, \gamma) : \gamma = \alpha + \beta^+, \ N\alpha \geq \gamma \geq \alpha\}.$$

When all points in this set are plotted in a three-dimensional positive space, they represent a surface without a boundary. To plot the surface C and C^+, we need to restrict either alpha or gamma to a finite range; otherwise the three-dimensional surface cannot be shown. In Fig. 1, we show the surface C and C^+ when alpha is restricted to a range $U \geq \alpha \geq L$. The corresponding plot for the restriction $U^* \geq \gamma \geq L^*$ is shown in Fig. 2. The surface obtained by considering constraints in a fixed-parameter model is identical to the surface portrayed by simulated points from random uniform distributions, if the number of simulations is sufficiently large. Therefore, any discussions regarding Figs. 1 and 2 are valid for both a graphical display (under a fixed-parameter model) and a simulation-based plot (under a random-parameter model).
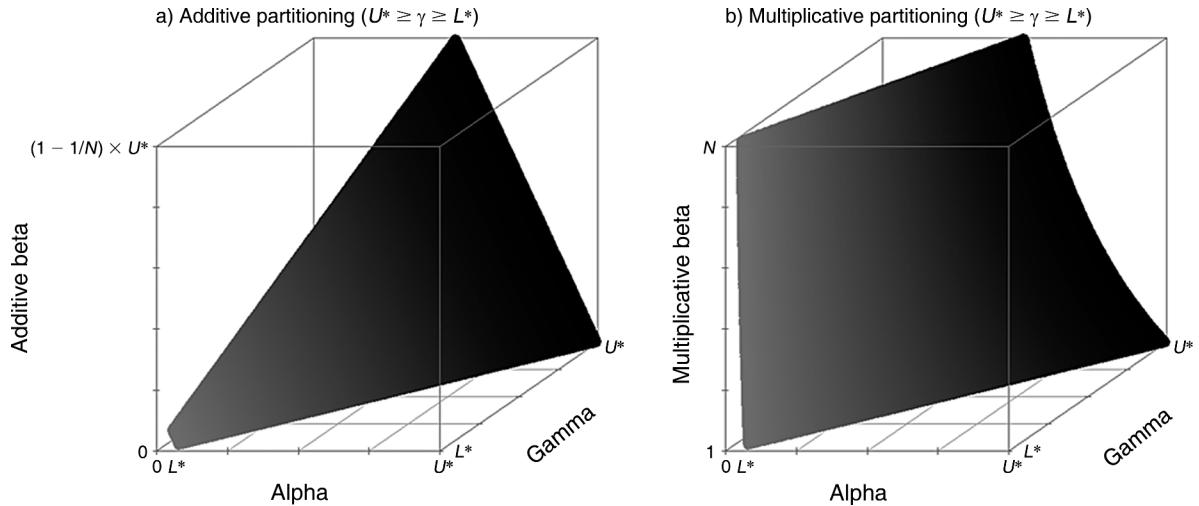
FIG. 2. Three-dimensional plot for three diversity components, where $N = 2$ (number of communities), $q = 0$ (order of Hill numbers), $L^* = 2$ (lower bound of gamma), and $U^* = 15$ (upper bound of gamma); for other terms, see Fig. 1. The surface is the same for both fixed-parameter and random-parameter models. (a) Additive partitioning with $U^* \geq \gamma \geq L^*$. The shaded area plots the surface $\{(\alpha, \beta^+, \gamma) : \gamma = \alpha + \beta^+, \gamma \geq \alpha \geq \gamma/N \text{ given } U^* \geq \gamma \geq L^*\}$. None of the three two-dimensional projections is a rectangle. (b) Multiplicative partitioning with $U^* \geq \gamma \geq L^*$. The shaded area plots the surface $\{(\alpha, \beta, \gamma) : \gamma = \alpha \times \beta, \gamma \geq \alpha \geq \gamma/N \text{ given } U^* \geq \gamma \geq L^*\}$. The projection onto the (β, γ)-plane is a rectangle, whereas the other two-dimensional projections are not rectangles.

Graphical display and simulation-based plots

As explained, when either alpha or gamma is restricted to a range, *conditional* relatedness or *conditional* dependence is induced for the other two diversity components (Table 2). Relatedness or dependence between any two diversity components can be shown not only by theoretically searching for constraints (as we described in previous sections and in Table 1), but also by graphs and simulation plots. To demonstrate the relationship between any two diversity components, we can simply project the three-dimensional surfaces in Figs. 1 and 2 onto any two-dimensional surface and examine whether the projected surface is a rectangle or not. In both figures, we only plot species richness ($q = 0$) for illustration, although for other values of q (especially $q = 1$ and 2), similar figures and discussion can be made.

In Fig. 1, when alpha is restricted to $U \geq \alpha \geq L$ (Baselga, Procedure 2), the three two-dimensional projections are similar to those in Baselga (2010: Fig. 2). For additive partitioning, none of the three two-dimensional projections is a rectangle, so all three diversity components are pairwise dependent (or related). For multiplicative partitioning, the projection onto the (α, β)-plane is a rectangle, showing that alpha and beta are unrelated, whereas the other two-dimensional projections are not rectangles. The projection onto the (β, γ)-plane is shown in Fig. 3 in order to see the meaning of conditional dependence and to see how the conditional dependence between β and γ vanishes in multiplicative partitioning as the condition is released. As shown in Fig. 3b, if we release the condition $U \geq \alpha \geq L$ by letting $U \rightarrow \infty$ and $L \rightarrow 0$, then the projected

surface on the (β, γ)-plane extends to a rectangle, whereas the (β^+, γ)-plane projection in Fig. 3a does not extend to a rectangle. Thus, β and γ become independent (unrelated), as indicated in Table 1, whereas the dependence (or relatedness) between β^+ and γ remains.

Similarly, in Fig. 2, when gamma is restricted to $U^* \geq \gamma \geq L^*$ (Baselga, Procedure 1), the three two-dimensional projections are similar to those in Baselga (2010: Fig. 1). For additive partitioning, none of the three two-dimensional projections is a rectangle. Thus all three diversity components are pairwise dependent (or related). For multiplicative partitioning, the projection onto the (β, γ)-plane is a rectangle, whereas the other two-dimensional projections are not rectangles. The projected surface onto the (α, β)-plane is shown in Fig. 4 in order to see the meaning of conditional dependence and to see how the conditional dependence between α and β vanishes in multiplicative partitioning as the condition is released. As shown in Fig. 4b, if we release the condition $U^* \geq \gamma \geq L^*$ by letting $U^* \rightarrow \infty$ and $L^* \rightarrow 0$, then the (α, β)-plane projection extends to a rectangle whereas the (α, β^+)-plane projection in Fig. 4a does not extend to a rectangle. Thus, α and β become independent (unrelated) as indicated in Table 1, whereas the dependence (or relatedness) between α and β^+ remains.

Proposed resolution

In Table 3, we list all fixed-parameter and random-parameter approaches by the authors in the Forum. In each case, we give the constraints and conditions that the authors considered in their papers. Based on Tables 1 and 2, all relatedness or dependence relationships between any two diversity components can be directly
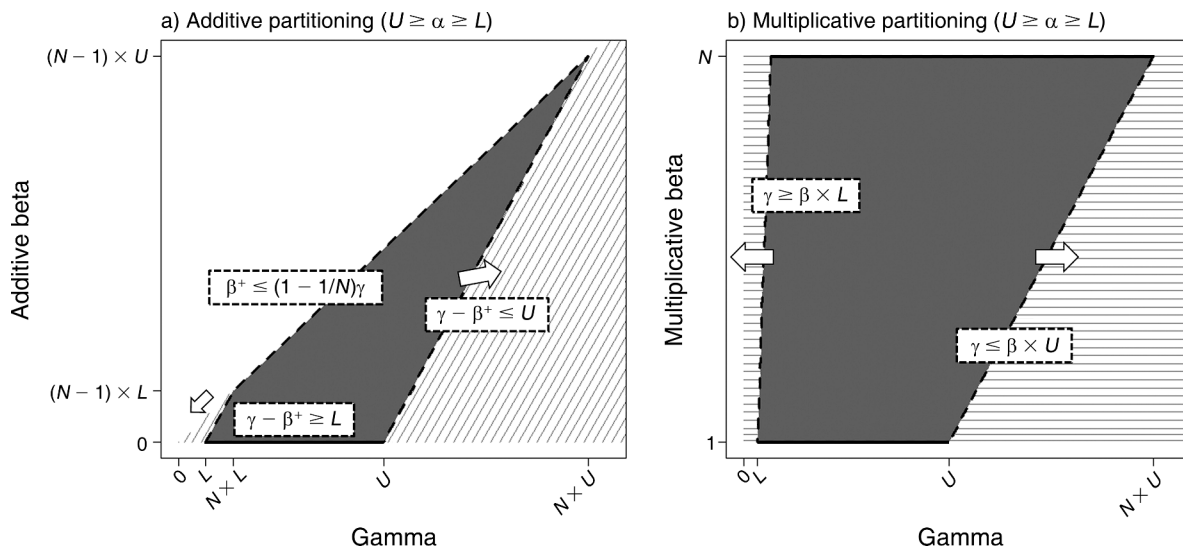
FIG. 3. The shaded area is the projection of the surface in Fig. 1 onto the (beta, gamma)-plane given the condition $U \geq \alpha \geq L$. For both partitioning methods, gamma and beta are conditionally dependent because the shaded area is not a rectangle. (a) Additive partitioning with $U \geq \alpha \geq L$. Since $U \geq \alpha \geq L \Rightarrow U \geq \gamma - \beta^+ \geq L$, the shaded area in the positive plane is determined by $\gamma - \beta^+ \geq L$ (due to setting a lower bound L) and $U \geq \gamma - \beta^+$ (due to setting an upper bound U) and $\beta^+ \leq (1 - 1/N)\gamma$ (due to constraint A given in Table 1). (b) Multiplicative partitioning with $U \geq \alpha \geq L$. Since $U \geq \alpha \geq L \Rightarrow \beta \times U \geq \gamma \geq \beta \times L$, the shaded area in the range $N \geq \beta \geq 1$ is determined by $\gamma \geq \beta \times L$ (due to setting a lower bound L), $\beta \times U \geq \gamma$ (due to setting an upper bound U). If we release the condition $U \geq \alpha \geq L$ by letting $U \to \infty$ and $L \to 0$, the shaded area extends to a line-shaded rectangle in panel (b), but in panel (a) the shaded area does not extend to a rectangle due to the constraint $(1 - 1/N)\gamma \geq \beta^+$.

obtained. Our conclusions in Table 3 exactly match with the findings of those reported in the Forum. Based on both theoretical and graphical/simulation-based approaches, now we can have a clear understanding of all authors' disagreements in the Forum (Table 3).

Veech and Crist's approach.—In Veech and Crist's (2010a) random-parameter simulations without fixing N, they concluded that alpha and beta are dependent in both additive and multiplicative partitioning schemes. The dependence between alpha and beta was not
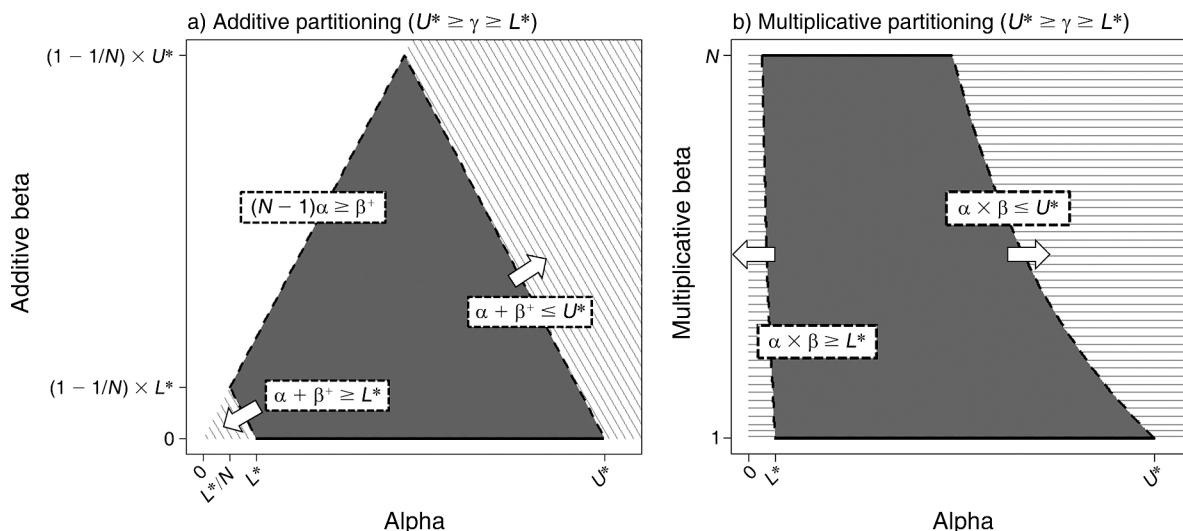

FIG. 4. The shaded area is the projection of the surface in Fig. 2 onto the (α, β)-plane given the condition $U^* \geq \gamma \geq L^*$. For both partitioning methods, alpha and beta are conditionally dependent because the shaded area is not a rectangle. (a) Additive partitioning with $U^* \geq \gamma \geq L^*$. Since $U^* \geq \gamma \geq L^* \Rightarrow U^* \geq \alpha + \beta^+ \geq L^*$, the shaded area in the positive plane is determined by $\alpha + \beta^+ \geq L^*$ (due to setting a lower bound L^*) and $U^* \geq \alpha + \beta^+$ (due to setting an upper bound U^*) and $(N - 1)\alpha \geq \beta^+$ (due to constraint A given in Table 1). (b) Multiplicative partitioning with $U^* \geq \gamma \geq L^*$. Since $U^* \geq \gamma \geq L^* \Rightarrow U^* \geq \alpha \times \beta \geq L^*$, the shaded area in the range $N \geq \beta \geq 1$ is determined by $\alpha \times \beta \geq L^*$ (due to setting a lower bound L^*) and $\alpha \times \beta \leq U^*$ (due to setting an upper bound U^*). If we release the condition $U^* \geq \gamma \geq L^*$ by letting $U^* \to \infty$ and $L^* \to 0$, the shaded area extends to a line-shaded rectangle in panel (b), but in panel (a) the shaded area does not extend to a rectangle due to the constraint $(N - 1)\alpha \geq \beta^+$.

TABLE 3. All fixed-parameter and random-parameter models in the Forum (Ellison 2010) on diversity partitioning.

Conditions/constraint	Additive ($\beta^+ = \gamma - \alpha$)	Multiplicative ($\beta = \gamma/\alpha$)
Veech and Crist random-parameter simulation (N is not fixed). First generate $\gamma \sim$ uniform (10, 1000), then generate $\alpha \sim$ uniform (1, γ). Range of $(\alpha, \gamma) = \{(\alpha, \gamma): \gamma \geq \alpha$ given $\alpha \geq 1$, $1000 \geq \gamma \geq 10\}$		
Condition (1a): $\alpha \geq 1$	(β^+, γ) conditionally dependent	(β, γ) conditionally dependent
Condition (2): $1000 \geq \gamma \geq 10$	(α, β^+) conditionally dependent	(α, β) conditionally dependent
Constraint: $\gamma \geq \alpha$	(α, γ) dependent	(α, γ) dependent
Jost fixed-parameter model (N fixed). Range of $(\alpha, \gamma) = \{(\alpha, \gamma): N\alpha \geq \gamma \geq \alpha$ given $\alpha \geq 1\}$		
Condition (1a): $\alpha \geq 1$	(β^+, γ) conditionally related;	(β, γ) conditionally related
Constraint (A): $N\alpha \geq \gamma \geq \alpha$	all three components pairwise related	(α, γ) related; (α, β) *unrelated*
Baselga random-parameter simulation, Procedure 1 (N fixed). First generate $\gamma \sim$ uniform (10, 1000), then generate $\alpha \sim$ uniform $(\gamma/N, \gamma)$. Range of $(\alpha, \gamma) = \{(\alpha, \gamma): \gamma \geq \alpha \geq \gamma/N$ given $1000 \geq \gamma \geq 10\}$		
Condition (2): $1000 \geq \gamma \geq 10$	(α, β^+) conditionally dependent;	(α, β) conditionally dependent
Constraint (A): $N\alpha \geq \gamma \geq \alpha$	all three components are pairwise dependent	(α, γ) dependent
		(β, γ) *independent*
Baselga random-parameter simulation, Procedure 2 (N fixed). First generate $\alpha \sim$ uniform (1, 100), then generate $\gamma \sim$ uniform $(\alpha, N\alpha)$. Range of $(\alpha, \gamma) = \{(\alpha, \gamma): N\alpha \geq \gamma \geq \alpha$ given $100 \geq \alpha \geq 1\}$		
Condition (1): $100 \geq \alpha \geq 1$	(β^+, γ) conditionally dependent;	(β, γ) conditionally dependent
Constraint (A): $N\alpha \geq \gamma \geq \alpha$	all three components are pairwise dependent	(α, γ) dependent
		(α, β) *independent*

Notes: The conditions (see Table 2) and constraint (see Table 1) for each model are listed in the first column. Diversities (α, γ, β, β^+) refer to Eqs. 3–8, and conclusions are valid for all $q \geq 0$.

induced by varying N, but rather by their restriction on gamma ($1000 \geq \gamma \geq 10$). They correctly noted that if the condition is released, alpha and beta are independent (see Table 3). Also, they found dependence between beta and gamma. This is because they set up a lower bound of 1 for alpha ($\alpha \geq 1$), i.e., Condition (1a) in Table 2. If alpha is allowed to be any positive number, then beta and gamma become independent for both partitioning methods.

Except for Veech and Crist, all the other authors in the Forum considered a fixed N and the results in this case are summarized as follows (see Table 3).

Jost's approach.—Jost obtained the relatedness of beta and gamma in the multiplicative fixed-parameter approach. This is because he imposed a condition $\alpha \geq L = 1$, which implies $\gamma \geq \beta$ and thus beta and gamma are conditionally related. See this condition in Fig. 3b and its effect on the projected plane. It is clear that the dependence between β and γ is due to $\gamma < N$. If we further restrict $\gamma \geq N$, then beta and gamma become unrelated in Jost's fixed-parameter model. Alpha is always unrelated to multiplicative beta.

Baselga's approach.—As Baselga (2010) rightly indicated, the conditional dependence between multiplicative alpha and beta in Baselga Procedure 1 is due to a restriction on gamma, and the conditional dependence between multiplicative gamma and beta in Baselga Procedure 2 is due to a restriction on alpha. In Table

2, we have explained how the dependence is induced. Figs. 3b and 4b graphically show why the conditional dependence vanishes if the restriction is released.

The debates about dependences between any two diversity components can thus be resolved: the reason that authors obtained seemingly contradictory conclusions regarding the dependence between any two diversity components is because each author imposed different conditions in the model or simulations. If none of the conditions are imposed, that is, if all conditional relatedness or dependences vanish, then the conclusions for all authors' models reduce to those in Table 1. For multiplicative partitioning, if alpha is allowed to be any positive number (or $\alpha \geq 1$, $\gamma \geq N$), not only are multiplicative beta and alpha independent (or unrelated) but also beta and gamma are independent (or unrelated). Only alpha and gamma are dependent (related). For additive partitioning, all three diversity components are pairwise dependent (or related).

ADDITIVE VS. MULTIPLICATIVE BETA

As discussed, multiplicative beta, which quantifies community diversity (i.e., the effective number of completely distinct communities), measures pure relative differentiation among communities. It ranges from 1 to N when weights are set equal (Table 1). Thus, it can be made into measures of relative compositional similarity or differentiation by transforming it (or its reciprocal)

onto the unit interval. There are many possible transformations of beta onto the unit interval, each addressing a different aspect of compositional similarity or differentiation (see Legendre and Legendre 1998, Koleff et al. 2003, Jost 2007, Gregorius 2010, Tuomisto 2010, Anderson et al. 2011, Jost et al. 2011). Three transformations will be discussed.

The additive beta quantifies the absolute magnitude of diversity increment or excess between a regional scale and a local scale. In Table 1, we have seen for fixed N how additive beta is dependent on alpha (or equivalently, on gamma); in Eqs. 10a and 10b, we have derived these dependence relationships. When ecologists aim to assess relative compositional differentiation among communities, it is clear now that these dependences should be removed. We will show that the resulting normalized measures when these dependences are removed turn out to be the same as those based on the multiplicative beta.

Similarity/differentiation measures from multiplicative beta

In order to compare relative compositional similarity or differentiation between communities across multiple regions with different numbers of communities, multiplicative beta (or its inverse) must be transformed onto the unit interval. We consider three such classes of similarity or differentiation measures:

1. *Relative turnover rate per community (Harrison et al. 1992, Jost 2006, 2007).*—This rate measures the proportion of a typical community that changes as one goes from one community to another in the region:

$$({}^{q}D_{\beta} - 1)/(N - 1). \qquad (12a)$$

This is a differentiation measure that is linear in beta and it ranges from 0 (no turnover among communities) to unity (each community is completely distinct from every other communities). Harrison et al. (1992) proposed this measure only for species richness ($q = 0$). Jost (2007) extended it to any order of Hill numbers.

2. *A class of homogeneity measures (MacArthur 1965, Jost 2006, 2007).*—This transformation is linear in the inverse of beta (the proportion of regional diversity contained in the average community):

$$^{q}S = (1/{}^{q}D_{\beta} - 1/N)/(1 - 1/N). \qquad (12b)$$

When $q = 0$, this is the multiple-community generalization of the Jaccard index (Koch 1957). When $q = 2$, this is the multiple-community generalization of the Morisita-Horn index (Morisita 1959, Horn 1966). The Jaccard and Morisita-Horn measures are members of the same family and are connected by a continuum of similarity measures, which differ only in their sensitivity to species' relative abundances.

3. *A class of overlap measures (Jost 2006, 2007, Chao et al. 2008).*—Based on a two-stage probabilistic approach, Chao et al. (2008) proposed the following transformation of multiplicative beta diversity and

obtained a measure called C_{qN}:

$$C_{qN} = [(1/{}^{q}D_{\beta})^{q-1} - (1/N)^{q-1}]/[1 - (1/N)^{q-1}] \qquad q \neq 1. \qquad (12c)$$

The special case of $N = 2$ was derived in Jost (2006, 2007). The measure C_{qN} can be expressed as a function of relative abundances; see Appendix A. This measure is unity when all communities are identical and 0 when all communities are completely distinct. It includes the multiple-community generalizations of the classical two-community Sørensen, Horn, and Morisita-Horn measures above three measures.

Consider the special case of $q = 0$. Let S denotes the total number of species in the combined communities, and $\bar{S}$ denotes the average number of species per community. Then multiplicative beta becomes ${}^{0}D_{\beta} = S/\bar{S}$ as defined in Eq. 7 for $q = 0$ (also see Whittatker 1972, Jost 2007). In this case, from Eq. 12c we have the following:

$$C_{0N} = (S/\bar{S} - N)/(1 - N) = 1 - ({}^{0}D_{\beta} - 1)/(N - 1) \qquad (13a)$$

which is the multiple-community version of the classical Sørenson index (Diserud and Ødegaard 2007). The measure C_{0N} is a decreasing function of Whittaker's beta and $1 - C_{0N}$ is the relative turnover rate per community of Harrison et al. (1992); see Eq. 12a. For $q = 1$, C_{1N} reduces to the multiple-community version of the Horn homogeneity measure (Chao et al. 2008):

$$C_{1N} = \lim_{q \to 1} C_{qN} = 1 - \frac{H_{\gamma} - H_{\alpha}}{\log N}$$

$$= \frac{1}{\log N} \sum_{i=1}^{S} \sum_{j=1}^{N} \left[\frac{p_{ij}}{N} \log \left(1 + \frac{\sum_{k \neq j} p_{ik}}{p_{ij}} \right) \right] \qquad (13b)$$

where H_{α} is the average entropy in an individual community, and H_{γ} is the entropy in the combined communities. For $q = 2$, C_{2N} reduces to the multiple-community version of the Morisita-Horn similarity index:

$$C_{2N} = 1 - \frac{H_{GS,\gamma} - H_{GS,\alpha}}{(1 - 1/N)(1 - H_{GS,\alpha})} = \frac{2 \sum_{i=1}^{S} \sum_{j < k} p_{ij} p_{ik}}{(N - 1) \sum_{i=1}^{S} \sum_{j=1}^{N} p_{ij}^{2}} \qquad (13c)$$

where $H_{GS,\alpha}$ and $H_{GS,\gamma}$ denote, respectively, the alpha and gamma Gini-Simpson index.

For $q > 0$, Eq. 12c shows that the measure C_{qN} is a *nonlinear* transformation of the multiplicative beta. Only a nonlinear transformation gives these measures the calibrated metric of a true overlap index (Chao et al. 2008). That is, the transformed index C_{qN} gives the true

overlap A/S for all orders of q if N communities each have S equally common species, with exactly A species shared by all of them, and the remaining species in each community not being shared with any other communities. No linear transformation of multiplicative beta diversity can achieve this goal. The measure C_{qN} quantifies the *effective average overlap per community*, i.e., the average percentage of overlapped species (species that are shared by all communities, as defined in the previous sense) in a community. Just as diversity profiles are used to characterize traditional diversity, Chao et al. (2008) suggest the use of a similarity profile $\{C_{qN}; q = 0, 1, 2, \ldots, N\}$ to describe similarity across N communities. We recommend that investigators calculate at least C_{0N}, C_{1N}, and C_{2N}; see Jost et al. (2011:81) for a numerical example with a plot.

Similarity/differentiation measures from additive beta

There is a simple relationship between additive beta, multiplicative beta, and alpha, i.e., $\beta^+ = \alpha(\beta - 1)$, equivalently $\beta = 1 + (\beta^+/\alpha)$. We can also have a relationship with gamma, i.e., $\beta^+ = \gamma(1 - 1/\beta)$, equivalently $\beta = 1/(1 - \beta^+/\gamma)$. Therefore, each of the three measures based on multiplicative beta (in Eqs. 12a–c) can be expressed as a function of (β^+, α) or a function of (β^+, γ). However, this approach will not reveal the role of dependence between β^+ and α (or dependence between β^+ and γ) in constructing relative similarity or differentiation measures from additive beta. Instead, we consider the dependence relationships in Table 1 and show how to remove dependence to obtain similarity or differentiation measures. From Table 1, additive beta depends not only on N but also on alpha (equivalently, on gamma); see also Figs. 3a and 4a. The basic constraint between alpha and additive beta is $(N - 1)\alpha \geq \beta^+$ (Eq. 10a). The basic constraint between gamma and additive beta is $(1 - 1/N)\gamma \geq \beta^+$ (Eq. 10b). Due to these constraints, when the goal is to assess the relative differentiation or similarity among communities, we cannot use additive beta to compare two or multiple regions with different alpha (or gamma) even if the numbers of communities are the same. The differences in additive beta values for two sets of communities may reflect the differences in alpha (or gamma) rather than the relative degree of compositional differentiation. Thus, dependences on alpha (or gamma) must be removed.

To remove the dependence on alpha and N due to the constraint $(N - 1)\alpha \geq \beta^+$, we can consider the normalized measure $\beta^+/\max(\beta^+) = \beta^+/[(N - 1)\alpha]$. It takes the value of 0 when the communities are identical and unity when communities are completely distinct. Notice the that normalized measure is

$$\frac{\beta^+}{(N-1)\alpha} = \frac{\beta - 1}{N - 1}$$

which is the relative diversity turnover rate in Eq. 12a. When $q = 0$, the above measure is $1 - C_{0N}$. In this case,

the constraint $(N - 1)\alpha \geq \beta^+$ is equivalent to

$$({}^0D_\gamma) - ({}^0D_\alpha) \leq (N-1)({}^0D_\alpha). \qquad (14)$$

To remove the dependence on gamma and N due to the constraint $(1 - 1/N)\gamma \geq \beta^+$, we consider the following normalized measure:

$$\frac{\beta^+}{(1 - 1/N)\gamma} = \frac{1 - 1/\beta}{1 - 1/N} = 1 - ({}^qS)$$

which is the complement of the homogeneity measure in Eq. 12b. When $q = 2$, this measure is $1 - C_{2N}$. In this case, the constraint $(1 - 1/N)\gamma \geq \beta^+$ is equivalent to

$$({}^2D_\gamma) - ({}^2D_\alpha) \leq (1 - 1/N)({}^2D_\gamma)$$
$$\Leftrightarrow ({}^2D_\alpha)^{-1} - ({}^2D_\gamma)^{-1} \leq (1 - 1/N)({}^2D_\alpha)^{-1}. \qquad (15)$$

The dependence relationships in Eqs. 14 and 15 can be generalized to any order of q. (See Appendix A for proof details). That is, for $0 \leq q < 1$, Eq. 14 can be generalized to

$$({}^qD_\gamma)^{1-q} - ({}^qD_\alpha)^{1-q} \leq (N^{1-q} - 1)({}^qD_\alpha)^{1-q}. \qquad (16a)$$

For $q > 1$, Eq. 15 can be generalized to

$$({}^qD_\alpha)^{1-q} - ({}^qD_\gamma)^{1-q} \leq (1 - N^{1-q})({}^qD_\alpha)^{1-q}. \qquad (16b)$$

In Eqs. 16a and b, we can make a similar normalization by dividing the left-hand side of each equation by the upper bound on the right-hand side. It turns out that both equations lead to the same formula, as shown on the left-hand side of Eq. 17. Moreover, for any $q \geq 0$ and $q \neq 1$, the resulting normalized formula is exactly $1 - C_{qN}$ (see Appendix A for proof details):

$$\frac{({}^qD_\gamma)^{1-q} - ({}^qD_\alpha)^{1-q}}{(N^{1-q} - 1)({}^qD_\alpha)^{1-q}} = 1 - C_{qN}. \qquad (17)$$

For $q = 1$, the limit tends to $1 - C_{1N} = (H_\gamma - H_\alpha)/\log N$; see Eq. 13b.

Therefore, we have shown that both multiplicative and additive approaches based on Hill numbers lead to the same similarity and differentiation measures. When we compare regions with the possibility of different number of communities, the normalized similarity (overlap) measures that satisfies the true overlap property for all orders of q is given by the measure C_{qN}, whether Hill numbers are decomposed additively or multiplicatively. It is important to point out that normalization is not a general cure for problems of dependence on alpha (or gamma). However, all the proposed normalizations in this paper turn out to be functions of multiplicative beta only. This is why we can conclude that the dependence on alpha (or gamma) can be removed via normalization.

TWO FORMULAS FOR ALPHA DIVERSITY

When community area or size needs to be taken into account, as in measuring regional heterogeneity (Horn 1966) instead of compositional differentiation, we can

consider a community weight w_j for the jth community, $j = 1, 2, \ldots, N$. This weight function can usually be taken to be the relative sizes (either in terms of area or total population) of the communities. When community weights are considered, the gamma diversity, which is a generalization of Eq. 4, has the following form:

$$^qD_\gamma = \left\{ \sum_{i=1}^{S} \left(\sum_{j=1}^{N} w_j p_{ij} \right)^q \right\}^{1/(1-q)} \qquad q \neq 1 \qquad (18)$$

(see Routledge 1979, Jost 2006, 2007). There are two proposed formulas for alpha diversity under multiplicative partitioning. Routledge (1979) proposed the following alpha diversity of order q based on Hill numbers:

$$^qD_{\alpha,R} = \left(\sum_{i=1}^{S} \sum_{j=1}^{N} w_j p_{ij}^q \right)^{1/(1-q)}. \qquad (19)$$

Tuomisto (2010) followed Routledge in advocating the use of this alpha. Jost (2007) derived (rather than defined) a different form of alpha diversity as the unique within-group component of regional diversity:

$$^qD_{\alpha,J} = \left(\sum_{i=1}^{S} \sum_{j=1}^{N} \frac{w_j^q}{w_1^q + \ldots + w_N^q} p_{ij}^q \right)^{1/(1-q)}. \qquad (20)$$

These two alpha diversities are identical in the case of equal community weights and are also identical in the case of $q = 1$ in the case of unequal community weights. When weights are considered, the differences between the two alpha diversities lie not only in the weights but also in some other critical aspects, to be discussed. Consider first the special case of $q = 0$. Routledge's alpha from Eq. 19 is a weighted mean of species richnesses, as follows:

$$^0D_{\alpha,R} = w_1 S_1 + w_2 S_2 + \ldots + w_N S_N \qquad (21a)$$

where S_j denotes the number of species in the jth community. Jost's alpha from Eq. 20 always reduces to the equal-weight mean of species richnesses, even when the actual weights are unequal:

$$^0D_{\alpha,J} = (S_1 + S_2 + \ldots + S_N)/N = \bar{S}. \qquad (21b)$$

This is the same as $^0D_\alpha$ in Eq. 3. The multiplicative beta $^0D_{\beta,R}$, using Routledge's alpha, becomes

$$^0D_{\beta,R} = S/(w_1 S_1 + w_2 S_2 + \ldots + w_N S_N). \qquad (22)$$

Jost's alpha leads to the following beta diversity:

$$^0D_{\beta,J} = S/[(S_1 + S_2 + \ldots + S_N)/N] = S/\bar{S} \qquad (23)$$

which is the same as $^0D_\beta$ in Eq. 7. From Eq. 22 and Eq. 23, we make the following observations:

1) The beta based on Routledge's alpha can take values larger than the number of communities N, causing an interpretational problem. For example, consider the special case of $N = 2$, $S_1 = 100$, $S_2 = 10$, $w_1 = 0.05$, and $w_2 = 0.95$. Assuming that the two communities are completely distinct (no shared species), then $^0D_{\beta,R} = 110/(0.05 \times 100 + 0.95 \times 10) = 7.6$, which is much greater than 2, the number of communities. In this case, $^0D_{\beta,J} = 2$, correctly implying that there are two completely distinct communities. Jost's beta in Eq. 23 is always between 1 and N and can be interpreted as "the effective number of completely distinct communities."

2) Jost's beta for $q = 0$ reduces to Whittaker's original beta based on species richness, whereas Routledge's beta does not.

3) Routledge's alpha in Eq. 21a is in terms of community weights, which generally depend on relative sizes, or equivalently, species abundances. This is inconsistent with the equal weights necessarily used in the gamma diversity (see Eq. 18 for $q = 0$). This is also inconsistent with the fact that species abundances do not count in Hill numbers, Tsallis (1988) entropy, or Rényi (1961) entropy for $q = 0$ in a single community. In contrast, Jost's alpha does not count species abundances for $q = 0$, and thus is consistent. More discussion on this aspect is given later.

4) In Appendix B, we show that Routledge's alpha and beta theoretically satisfy a constraint and thus are dependent (or related), whereas Jost's alpha and beta are independent (or unrelated). A simulation is also shown in Appendix B to confirm our theoretical conclusion.

These findings show that Jost's alpha in Eq. 20 is the proper choice when the goal is to partition regional diversity into independent within- and between-group components.

CONCLUSION AND DISCUSSION

In this paper, we have clarified the meaning of independence (or unrelatedness) of alpha diversity and beta diversity. Table 1 gives a summary of the dependence relations for any pair of diversity components, for both additive and multiplicative partitioning schemes based on Hill numbers for $\alpha \geq 0$. The conclusions in Table 1 can be justified by both theory and empirical simulations. Thus a consensus may be reached. When N is fixed, all three components in additive partitioning are pairwise dependent (or related); in multiplicative partitioning, alpha and beta are independent (or unrelated), beta and gamma are also independent (or unrelated), and only alpha and gamma are dependent (or related). If alpha diversity is restricted to be greater than or equal to unity, and gamma is not less than the number of communities (which is often the case in applications), then all conclusions remain the same.

In comparing the relative compositional similarity or differentiation among multiple sets of communities, both multiplicative beta and additive beta should be properly normalized, because multiplicative beta de-

pends on the number of communities, and additive beta depends additionally on alpha diversity (equivalently, on gamma diversity). We have shown that when the two decomposition methods are properly transformed, both lead to the same similarity and differentiation measures, including the multiple-community generalization of the Sørenson, Jaccard, Horn, and Morisita-Horn measures. This bridges two decomposition frameworks and emphasizes the generality of the overlap measure C_{qN} for quantifying compositional similarity or differentiation among communities.

To select a proper formula for alpha diversity, we have given some reasons to suggest the use of the alpha diversity derived by Jost (2007) instead of the one adopted by Routledge (1979) and Tuomisto (2010). The most important justification is that only Jost's alpha is independent of (or unrelated to) beta diversity. When only species incidence (presence–absence) information is available, the commonly used incidence-based (or equivalently, richness-based) alpha diversity is simply $\bar{S}$ (Eq. 21b), and beta diversity is $S/\bar{S}$ (Eq. 23); see Whittaker (1972). As discussed earlier, if Routledge's alpha is applied to form a multiplicative beta, then the beta diversity of order zero is in terms of abundances and is different from the incidence-based beta diversity. In contrast, if Jost's alpha is applied to form a beta, then the alpha, beta, and gamma diversities of order 0 do not count species abundances and are the same as the incidence-based alpha, beta, and gamma diversities. Thus, another advantage of using Jost's alpha is that incidence-based measures are simply the abundance-based measures of order zero. Then it is not necessary to define additional formulas and terminology for incidence- or richness-based alpha, beta, and related measures. For example, richness-based alpha, beta, and gamma diversities are simply diversity-based alpha, beta, and gamma diversities of order zero. This will help to simplify diversity theory and also may help to avoid unnecessary proliferation of terminology.

We suggest that multiplicative beta be used to measure the heterogeneity of a region. The areas of each community are important for this question and should be used (either alone or in combination with density) for the community weights. A decomposition that takes into account unequal weights is only possible for $q = 1$ (see formula in Jost 2007). The result is in units of the effective number of completely distinct communities in the region; dividing by the area of the region gives the effective number of distinct communities per unit of area. We recommend that the overlap measure C_{qN} be used to measure the relative compositional similarity between communities; the areas or densities do not matter for this question, and statistical weights of the communities should all be set equal in the calculation of alpha and gamma. As shown here, both multiplicative and additive beta can be normalized to yield C_{qN}. This gives the effective proportion of a typical community's species that overlaps with all other communities. It ranges from 0 to 1.00. This will be most relevant for identifying community relationships or measuring differences in ecosystem functioning between assemblages. The complement of this, $1 - C_{qN}$, gives a robust measure of relative differentiation between communities, the effective proportion of a typical community that is endemic to that community. We recommend additive beta divided by $(N - 1)$ to quantify the effective number of endemic species per community. This quantity might be especially useful in conservation analyses.

The Forum was focused on traditional Hill numbers, which do not take species evolutionary history into account. As Ricotta (2010:1982) pointed out "... the next step will now consist in extending this partitioning scheme to diversity measures that incorporate information about the degree of ecological similarity between species ..." Chao et al. (2010) and Leinster and Cobbold (2012) have recently generalized Hill numbers to a class of measures that incorporate phylogenetic distances between species. Also, it is important to notice that only species *relative* abundances are involved in obtaining Hill numbers. Species *absolute* abundances play no role in traditional diversities. Therefore, a three-species community with absolute abundances {2, 5, 6} has the same diversity profile as another three-species community with absolute abundances {200, 500, 600}. From an ecosystem functioning viewpoint, Ricotta (2003) argued that, given two communities having the same relative abundances, the one with larger absolute abundances should be more diverse. We are currently working on extending Hill numbers to include species absolute abundances. The meaning of "independence" and the bridge between the two partitioning frameworks discussed in this paper may be helpful for future work on the decomposition of phylogenetic diversity and extended Hill numbers.

All of our discussion is basically at a community or parameter level. That is, all diversity and similarity/differentiation measures are in terms of true community parameters (species richness and species relative abundances). We assume that these parameters are known in our discussion. At this level, data are not involved. However, in practice, all measures need to be estimated from sampling data. In the Forum, Wilsey (2010) applied diversity decomposition to some real field data. The estimation issue from sampling data is important in practice, and statistical estimation methods should be considered. For example, at the community level, the diversity profile of Hill numbers can be compared for any two communities. However, two diversity profiles obtained from sample data randomly selected from each community cannot be directly compared. Statistical estimation (Gotelli and Chao 2012) or standardization methods such as rarefaction and extrapolation (Colwell et al. 2012) should be applied. These considerations also apply to the estimation or standardization of alpha,

beta, and gamma diversities, as well as similarity/ differentiation measures. We briefly summarize some key points in Appendix C; see Gotelli and Chao (2012) for more estimation details.

LITERATURE CITED

Anderson, M. J., et al. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Baselga, A. 2010. Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. Ecology 91:1974–1981.

Chao, A., C.-H. Chiu, and L. Jost. 2010. Phylogenetic diversity measures based on Hill numbers. Philosophical Transactions of the Royal Society B 365:3599–3609.

Chao, A., and L. Jost. 2012. Diversity measures. Pages 203–207 *in* A. Hastings and L. Gross, editors. Encyclopedia of theoretical ecology. University of California Press, Berkeley, California, USA.

Chao, A., L. Jost, S.-C. Chiang, Y.-H. Jiang, and R. L. Chazdon. 2008. A two-stage probabilistic approach to multiple-community similarity indices. Biometrics 64:1178–1186.

Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.

Diserud, O. H., and F. F. Ødegaard. 2007. A multiple-site similarity measure. Biology Letters 3:20–22.

Ellison, A. M. 2010. Partitioning diversity. Ecology 91:1962–1963.

Gotelli, N. J., and A. Chao. 2012. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. *In* S. A. Levin, editor. The encyclopedia of biodiversity. Second edition. Elsevier, New York, New York, USA, *in press*.

Gregorius, H. R. 2010. Linking diversity and differentiation. Diversity 2:370–394.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta diversity on geographic gradients in Britain. Journal of Animal Ecology 61:151–158.

Hill, M. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist 100:419–424.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Jost, L. 2010. Independence of alpha and beta diversities. Ecology 91:1969–1974.

Jost, L., A. Chao, and R. L. Chazdon. 2011. Compositional similarity and beta diversity. Pages 66–84 *in* A. Magurran and B. McGill, editors. Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, UK.

Jost, L., P. DeVries, T. Walla, H. Greeney, A. Chao, and C. Ricotta. 2010. Partitioning diversity for conservation analyses. Diversity and Distributions 16:65–76.

Jurasinski, G., V. Retzer, and C. Beierkuhnlein. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia 159:15–26.

Koch, L. F. 1957. Index of biotal dispersity. Ecology 38:145–148.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72:367–382.

Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76:5–13.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier B. V., Amsterdam, The Netherlands.

Leinster, T., and C. A. Cobbold. 2012. Measuring diversity: the importance of species similarity. Ecology 93:477–489.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Reviews 40:510–533.

Magurran, A. E., and B. J. McGill, editors. 2011. Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, UK.

Moreno, C. E., and P. Rodríguez. 2010. A consistent terminology for quantifying species diversity? Oecologia 163:279–282.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoires of the Faculty of Science, Kyushu University, Series E 3:65–80.

Rényi, A. 1961. On measures of entropy and information. Pages 547–560 *in* J. Neyman, editor. Proceedings of the Fourth Berkeley Symposium on Mathematical Statistics and Probability. Volume 1. University California Press, Berkeley, California, USA.

Ricotta, C. 2003. Parametric scaling from species relative abundances to absolute abundances in the computation of biological diversity: a first proposal using Shannon's entropy. Acta Biotheoretica 51:181–188.

Ricotta, C. 2010. On beta diversity decomposition: Trouble shared is not trouble halved. Ecology 91:1981–1983.

Routledge, R. 1979. Diversity indices: which ones are admissible? Theoretical Population Biology 76:503–515.

Tsallis, C. 1988. Possible generalization of Boltzmann-Gibbs statistics. Journal of Statistical Physics 52:480–487.

Tuomisto, H. 2010. A diversity of beta diversity: straightening up a concept gone awry. Part 1: defining beta diversity in terms of alpha and gamma diversity. Ecography 33:2–22.

Veech, J. A., and T. O. Crist. 2010a. Diversity partitioning without statistical independence of alpha and beta. Ecology 91:1964–1969.

Veech, J. A., and T. O. Crist. 2010b. Toward a unified view of diversity partitioning. Ecology 91:1988–1992.

Veech, J. A., K. S. Summerville, and T. O. Crist. 2002. The additive partitioning of species diversity: recent revival of an old idea. Oikos 99:3–9.

Vellend, M. 2001. Do commonly used indices of β-diversity measure species turnover? Journal of Vegetation Science 12:545–552.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 12:213–251.

Wilsey, B. J. 2010. An empirical comparison of beta diversity indices in establishing prairies. Ecology 91:1984–1988.

SUPPLEMENTAL MATERIAL

Appendix A

Derivational details for Eqs. 16a, 16b, and 17 (*Ecological Archives* E093-195-A1).

Appendix B

More comparisons of the two formulas for alpha diversity (*Ecological Archives* E093-195-A2).

Appendix C

Statistical estimation issues (*Ecological Archives* E093-195-A3).