Review & synthesis

Ecography 33: 2–22, 2010
doi: 10.1111/j.1600-0587.2009.05880.x

Subject Editor: Robert K. Colwell. Accepted 18 November 2009

A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity

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The term *beta diversity* has been used to refer to a wide variety of phenomena. Although all of these encompass some kind of compositional heterogeneity between places, many are not related to each other in any predictable way. The present two-part review aims to put the different phenomena that have been called beta diversity into a common conceptual framework, and to explain what each of them measures. In this first part, the focus is on defining a beta component of diversity. This involves deciding what diversity is and how the observed total or gamma diversity (γ) is partitioned into alpha (α) and beta (β) components. Several different definitions of ''beta diversity'' that result from these decisions have been used in the ecological literature. *True beta diversity* is obtained when the total effective number of species in a dataset (*true gamma diversity* γ) is multiplicatively partitioned into the effective number of species per compositionally distinct virtual sampling unit (*true alpha diversity* α_d) and the effective number of such compositional units ($\beta_{Md} = \gamma/\alpha_d$). All true diversities quantify the effective number of types of entities. Because the other variants of ''beta diversity'' that have been used by ecologists quantify other phenomena, an alternative nomenclature is proposed here for the seven most popular beta components: regional-to-local diversity ratio, two-way diversity ratio, absolute effective species turnover (=regional diversity excess), Whittaker's effective species turnover, proportional effective species turnover, regional entropy excess and regional variance excess. In the second part of the review, the focus will be on how to quantify these phenomena in practice. This involves deciding how the sampling units that contribute to total diversity are selected, and whether the entity that is quantified is all of ''beta diversity'', a specific part of ''beta diversity'', the rate of change in ''beta diversity'' in relation to a given external factor, or something else.

In a seminal paper, Whittaker (1960, p. 320) defined *beta diversity* as ''The extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments''. He then proceeded to quantify beta diversity in different ways. His first two cases concerned Jaccard index (example 1) and percentage similarity (example 2) values between vegetation samples differing in geological formation and/or local moisture conditions. His third example quantified beta diversity as the ratio of gamma diversity (diversity in a set of sampling units) to alpha diversity (average diversity within sampling units) within each geological formation. His fourth example quantified beta diversity as the number of half-change units, the half-change unit being the distance along a transect by which similarity between two sampling units decreases to one-half of the value estimated for similar environments.

Obviously, Whittaker (1960) did not have an exact definition of beta diversity in mind, but used the term in a rather vague sense to refer to compositional heterogeneity among places. His verbal definition of beta diversity was broad, and each new example added a new phenomenon to it. All of the quantitative definitions are ratios that can be interpreted as unitless, but in fact their measurement units are species/species (example 1), (% abundance)/(% abundance) (example 2), (unit of diversity index)/(unit of diversity index) (example 3) and (unit of external gradient)/(unit of external gradient) (example 4). Under these definitions, beta diversity can be calculated for sampling units representing different habitat classes (examples 1 and 2), the same habitat class (example 3), or a gradient that has not been divided into habitat classes (example 4). Beta diversity may be explicitly dependent on a specified external gradient (distance along a transect in example 4) or not (examples 1, 2 and 3). Either species presence-absence data (examples 1 and 4) or quantitative abundance data (examples 2, 3 and 4) can be used in different mathematical formulae.

Whittaker (1960) introduced the term beta diversity (β) together with *alpha diversity* (α) and *gamma diversity* (γ). Both α and γ represent species diversity, but α is the mean species diversity at the local, within-site or within-habitat scale, whereas γ is the total species diversity at the regional

or landscape scale. Cody (1975) redefined *beta diversity* as the rate of compositional turnover along a habitat gradient within one geographical region, and *gamma diversity* as the rate of compositional turnover with geographical distance within one habitat. Bratton (1975) also used the term beta diversity to refer to the rate of species turnover along a gradient. Whittaker (1977) accepted this expansion of *beta diversity*, which then became the ''extent or rate of change in composition''. To account for different spatial scales, Whittaker (1977) proposed a hierarchical nomenclature in which alpha diversity refers to within-habitat diversity, beta diversity to among-habitat differentiation in a landscape, gamma diversity to total within-landscape diversity, *delta diversity* to among-landscape differentiation in a region, and *epsilon diversity* to total within-region diversity.

No wonder, therefore, that researchers have had a hard time agreeing on which quantitative interpretation of beta diversity is the correct one. Sources of contention include how beta diversity should be calculated, whether it should be measured within habitats or between habitats, and what spatial scales are appropriate. Several attempts have been made to tie alpha and gamma diversity to specific spatial scales (reviewed in Whittaker et al. 2001 and Magurran 2004), but little consensus has emerged on this point. However, usually researchers are interested in habitats and regions so extensive that full species inventories are a practical impossiblity, so that obtaining accurate estimates of alpha and gamma diversity is a major concern (Colwell and Coddington 1994, Plotkin and Muller-Landau 2002, Chao et al. 2006).

Here I do not wish to dwell on how to delimit *local*, *regional* or *habitat* in practice, or on issues of data representativeness. Although these are important questions, the logical definition of the phenomenon that is to be measured needs to be established before it is useful to discuss practical sampling problems. Therefore I will treat all diversity components as properties of a dataset: once it has been decided which data points form the dataset of interest, all diversity components can be exactly quantified for that dataset. In this context, spatial scales are arbitrary and can be selected freely. The data need to come from discrete sampling units embedded in a study region, but whether lag (distance between neighboring sampling units) is small or large is irrelevant. The extent of the study corresponds to the size of the study region and the grain to the size of the sampling unit. Delta and epsilon diversities become unnecessary, because they simply refer to beta and gamma diversity, respectively, in a study system with large grain and extent. Grain and extent affect the numerical values of the diversity components, and lag needs to be taken into account when extrapolating results from an existing dataset to uninventoried areas. These issues will be discussed in the second part of the present review (Tuomisto 2010), once the basic concepts have been defined.

Defining *beta diversity* is the main topic of the present paper. All variants of the umbrella concept encompass some kind of heterogeneity, differentiation or complementarity, but they actually refer to quite different phenomena. Some of these phenomena vary independently of each other among datasets, and ''beta diversity'' values based on different variants may therefore not be correlated. The situation is similar to that for the umbrella concept *size*. If we did not have separate words for weight, length, height, area and volume, discussions on size would become very confusing. The situation would become even worse if the term size were not only used for both weight and height, but also for growth rate. For example, consider animal A whose size is 100 cm, and animal B whose size is 10 kg. Which animal is bigger? It is impossible to say, because the given values are not commensurate. If the weight of A is revealed to be 5 kg, we know that B is heavier than A. But finding out that the size of B is 100 allows no conclusions, because we do not know if the unit of measurement was inches, meters, grams, pounds or something else. Furthermore, different aspects of size may rank animals differently; a snake that is larger than an elephant by the body length criterion is probably smaller by the body height or body weight criterion. If ranking is done using growth rate as the size criterion, it may be found that the younger the animal, the ''larger'' it is, and that in old animals ''size'' can even obtain a negative value.

Comparing measurements based on different variants of the umbrella concept is equally useless in the case of ''beta diversity''. Some variants of ''beta diversity'' are ratios in which the measurement units cancel out, whereas the measurement units in others can be, for example, virtual sampling units, species, (virtual species)$^{-1}$, bits, species per unit sampling effort, km^{-1}, species per km or species per unit habitat gradient. Because all variants of ''beta diversity'' are both multivariate and abstract, such crucial differences among them are much more difficult to spot than in the case of size. Consequently, the beta diversity literature is replete with studies that commit errors analogous to drawing conclusions on height on the basis of results on weight, or to comparing how two studies ranked different animal species without noticing that one study had measured body length whereas the other had measured the rate at which the animals' weight increased over time.

Many authors have commented on the confusion around the concept of beta diversity (Gray 2000, Vellend 2001, Koleff et al. 2003a, b, Novotny and Weiblen 2005). The most thorough review to date seems to be that by Jurasinski et al. (2009), who classified several beta diversity concepts into two categories. My aim in the present review is to explain what those and many other variants of ''beta diversity'' actually mean, and to put them into a common conceptual framework. It is crucial to use a metric that appropriately represents the phenomenon of interest, and knowledge about the logical relationships among alternatives can help in making that choice.

In the present two-part review, ''beta diversity'' variants are thought of as either 1) basic definitions or 2) approaches to applying a basic definition to a particular dataset. The variants of the first category will be discussed in the first part of the review and those of the second category in the second part. A basic definition specifies what ''diversity'' is and how the total or gamma ''diversity'' is partitioned into alpha and beta components. Once a basic definition has been chosen, it needs to be decided how the sampling units are selected, and whether to quantify all of ''beta diversity'', a part of ''beta diversity'', the rate of change in

"beta diversity" in relation to some external factor, or someting else. Each approach leads to quantifying a different phenomenon, but all have been called *beta diversity*. To facilitate more accurate communication in the future, other names will here be proposed for all variants other than true beta diversity.

The starting point: what is diversity?

Diversity in relation to a single classification

In order to measure diversity in a dataset of interest, the entities of which it is composed (such as individuals) need to be classified into types (such as species). Let us call the classification of individuals (or other appropriate units of abundance) into species the *γ-classification*. Total diversity in relation to the γ-classification is *gamma diversity* (γ), or total species diversity. The simplest measure of diversity is the number of types recognised, in this case species richness *S*. This equals the number of columns in a sites by species table (Table 1). In the present paper, *S* itself is used as a unitless number; the annotation *S* sp will be used, when necessary, to make the measurement unit (species) explicit. The number of types has the important doubling property, which can be understood by a thought experiment (Hill 1973, Wilson and Shmida 1984). Imagine that each column in Table 1 is split into two columns, and each proportional abundance value of the original species is evenly divided between the two new species. Intuitively, the species diversity of the dataset has thereby doubled, and so has its species richness.

If all species are equally abundant, each of their proportional abundances (column totals in Table 1) equal $1/S$. Mean proportional abundance then also equals $1/S$. When proportional abundances vary, their mean can be expressed $1/S_E$. The inverse of this mean, S_E, is the number of equally-abundant virtual species (*effective species*) in the dataset, also known as the effective number of species or species diversity (MacArthur 1965, Hill 1973, Jost 2006). The measurement unit becomes sp_E, where subscript "E" refers to effective. True species diversity hence quantifies *how many effective species the dataset represents, given the mean proportional abundance of the actual species*. In fact, diversity in general can be defined in this way: *the true diversity of the types of entities of interest is the inverse of the mean of their proportional abundances*.

A mean can be calculated in different ways, with some kinds of mean giving more weight to small values and others to large values. The weighted generalised mean with exponent $q-1$ allows a balance to be chosen that is appropriate for the questions at hand (Hill 1973):

$$\bar{p}_i = \sqrt[q-1]{\sum_{i=1}^{S} p_i p_i^{q-1}} = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(q-1)}$$

Here p_i is the proportional abundance of the ith species (see Table 1 for annotation of proportional abundances). This expression becomes the harmonic mean when $q=0$, the geometric mean in the limit as q approaches unity, the arithmetic mean when $q=2$ and the maximum value in the limit as q approches infinity. Each species is nominally weighted by the proportion of the data it contributes to the dataset, i.e. by p_i itself, but the effective species weights also depend on q. When $q=1$, the effective weights equal the nominal weights, and each species i affects the mean exactly in proportion to p_i. As q is increased, the most abundant species gain more effective weight and the mean gradually approaches the largest p_i value in the dataset no matter how many species the dataset contains. As q is decreased, the least abundant species gain more effective weight, such that at $q=0$ all effective weights are the same and the mean equals $1/S$ no matter how unequal the p_i values. When $q<0$, the least abundant species would get more effective weight than the most abundant species, and the effective number of species would exceed the actual number of

Table 1. A raw data table indicating how the *m* observed entities of interest have been classified into species according to the γ-classification (columns) and into sampling units (SU) according to the ω-classification (rows). The absolute abundance of species *i* in sampling unit *j* is annotated m_{ij}, and each cell value in the table (p_{ij}) gives this as a proportion of the total abundance *m* of all species in the dataset. Absolute abundance can be quantified using any measure that is appropriate for the questions at hand, for example number of individuals, surface area or biomass. The row totals show the proportion of the total abundance contributed by sampling unit *j*, i.e. the weight of sampling unit *j* in the dataset. The column totals show the proportion of the total abundance contributed by species *i*, i.e. the weight of species *i* in the dataset. The proportional abundance of species *i* within the limits of sampling unit *j* is $p_{i|j}=p_{ij}/w_j$ from which follows that $p_{ij}=w_j p_{i|j}$.

	Sp 1	Sp 2	Sp *i*	Sp *S*	Sampling unit weight
SU 1	$p_{11}=m_{11}/m$	$p_{21}=m_{21}/m$	$p_{i1}=m_{i1}/m$	$p_{S1}=m_{S1}/m$	$w_1=\sum_{i=1}^{S}\frac{m_{i1}}{m}$
SU 2	$p_{12}=m_{12}/m$	$p_{22}=m_{22}/m$	$p_{i2}=m_{i2}/m$	$p_{S2}=m_{S2}/m$	$w_2=\sum_{i=1}^{S}\frac{m_{i2}}{m}$
SU *j*	$p_{1j}=m_{1j}/m$	$p_{2j}=m_{2j}/m$	$p_{ij}=m_{ij}/m$	$p_{Sj}=m_{Sj}/m$	$w_j=\sum_{i=1}^{S}\frac{m_{ij}}{m}$
SU *N*	$p_{1N}=m_{1N}/m$	$p_{2N}=m_{2N}/m$	$p_{iN}=m_{iN}/m$	$p_{SN}=m_{SN}/m$	$w_N=\sum_{i=1}^{S}\frac{m_{iN}}{m}$
Species weight	$p_1=\sum_{j=1}^{N}\frac{m_{1j}}{m}$	$p_2=\sum_{j=1}^{N}\frac{m_{2j}}{m}$	$p_i=\sum_{j=1}^{N}\frac{m_{ij}}{m}$	$p_S=\sum_{j=1}^{N}\frac{m_{Sj}}{m}$	$\sum_{j=1}^{N}\sum_{i=1}^{S}\frac{m_{ij}}{m}=1$

species observed, so q must logically be restricted to nonnegative values.

True diversity is the inverse of $\bar{p}_i$ and equals (Hill 1973)

$$ {}^{q}D_{\gamma} = \bar{p}_i^{-1} = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)} = ({}^{q}\lambda_{\gamma})^{1/(1-q)} $$

where subscript "γ" indicates that the calculations are based on the γ-classification (see Table 2 for annotation of derived variables). When either $q = 0$ or all p_i are equal, then $S_E = S$ and hence ${}^{q}D_{\gamma} = S\ \mathrm{sp}_E$. Otherwise, $S_E < S$ and therefore ${}^{q}D_{\gamma} < S\ \mathrm{sp}_E$. The difference between the actual and effective number of species increases as the value of q and/or the inequality among the p_i values increase.

The term ${}^{q}\lambda_{\gamma} = \Sigma_{i=1}^{S} p_i^q = \bar{p}_i^{q-1}$, known as the *basic sum*, is important because most of the popular species diversity indices can be derived from it (Hill 1973, Keylock 2005). For example, ${}^{0}\lambda_{\gamma}$ equals species richness, ${}^{2}\lambda_{\gamma}$ Simpson's index, $1/{}^{2}\lambda_{\gamma}$ the inverse Simpson index, $1 - {}^{2}\lambda_{\gamma}$ the Gini-Simpson index and ${}^{\infty}\lambda_{\gamma}$ the Berger-Parker index. The

Table 2. Summary of the annotation used for the variables derived from species proportional abundances. Synonymous expressions are listed on the same line. Annotation related to the proportional abundances themselves is explained in Table 1.

Symbol			Explanation
$\bar{p}_i$	$\left(\sum_{i=1}^{S} p_i^q \right)^{1/(q-1)}$	$\sqrt[q-1]{\sum_{i=1}^{S} p_i p_i^{q-1}}$	mean proportional species abundance; the weighted generalised mean with exponent $q-1$ of the p_i values
${}^{q}\lambda_{\gamma}$	$\sum_{i=1}^{S} p_i^q$	$\bar{p}_i^{q-1}$	basic sum of order q in relation to the γ-classification: the sum of p_i^q values over all species i, or mean proportional species abundance raised to the power $q-1$
${}^{q}D$	$1 / \bar{p}_i$	${}^{q}\lambda^{1/(1-q)}$	true diversity of order q: the inverse of mean proportional abundances of the types of interest, or the numbers equivalent of ${}^{q}\lambda$
H'	$\log({}^{1}D)$	$\log(1 / \bar{p}_i)$	Shannon entropy: the logarithm of true diversity of order 1, or the logarithm of the inverse of the geometric mean of the proportional abundances of the types of interest
γ'			the raw value of a species diversity index as calculated using the entire dataset, e.g. ${}^{q}\lambda_{\gamma}$ or $H'\gamma$
α'			the alpha component obtained when partitioning γ'
β'			the beta component obtained when partitioning γ'
${}^{q}D_{\gamma}$	$\gamma = 1 / \bar{p}_i$	${}^{q}\lambda_{\gamma}^{1/(1-q)}$	true gamma diversity: total effective number of species in the dataset (measurement unit: effective species or sp_E)
$\bar{p}_{(i\|j)j}$	$\sqrt[q-1]{\sum_{i=1}^{S} p_{i\|j} p_{i\|j}^{q-1}}$		mean proportional species abundance within sampling unit j; the weighted generalised mean with exponent $q-1$ of the $p_{i\|j}$ values corresponding to sampling unit j
${}^{q}D_{\gamma j}$	$1 / \bar{p}_{(i\|j)j}$	$\gamma_j = {}^{q}\lambda_{\gamma j}^{1/(1-q)}$	gamma diversity (= effective number of species) within sampling unit j (measurement unit: sp_E)
$\bar{p}_{(i\|j)\mathrm{all}}$	$\sqrt[q-1]{\sum_{j=1}^{N} \sum_{i=1}^{S} p_{ij} p_{i\|j}^{q-1}}$		mean proportional species abundance in the dataset; the weighted generalised mean with exponent $q-1$ of all $p_{i\|j}$ values
α_t	${}^{q}\bar{D}_{\gamma j} = \bar{\gamma}_j$	$1 / \bar{p}_{(i\|j)\mathrm{all}}$	mean species diversity within sampling units: weighted generalised mean with exponent $1-q$ of the ${}^{q}D_{\gamma j}$ values with w_j used as weights (measurement unit: sp_E)
α_d	${}^{q}D_{\alpha}$	α_t/CU	true alpha diversity: effective number of species per virtual sampling unit of mean species diversity, or per compositional unit (measurement unit: $\mathrm{sp}_E/\mathrm{CU}$)
α_R	${}^{q}D_{\gamma\omega'/\omega}$	${}^{q}D_{\gamma\omega'}/{}^{q}D_{\omega}$	effective number of species abundance values per effective sampling unit (measurement unit: $\mathrm{sp}_E\mathrm{SU}_E/\mathrm{SU}_E$)
β_{Md}	${}^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$	γ/α_d	true beta diversity: number of compositional units in the dataset (measurement unit: CU)
β_{Mt}	${}^{q}D_{\gamma/\bar{\gamma}j} = {}^{q}D_{\gamma}/{}^{q}\bar{D}_{\gamma j}$	γ/α_t	regional-to-local diversity ratio (measurement unit: $\mathrm{sp}_E/\mathrm{sp}_E$)
β_R	${}^{q}D_{\gamma}\ {}^{q}D_{\omega}/{}^{q}D_{\gamma\omega'}$	γ/α_R	two-way diversity ratio (measurement unit: $\mathrm{sp}_E\mathrm{SU}_E/\mathrm{sp}_E\mathrm{SU}_E$)
β_{At}	${}^{q}D_{\gamma} - {}^{q}\bar{D}_{\gamma j}$	$\gamma - \alpha_t$	regional diversity excess; absolute effective species turnover (measurement unit: sp_E)
β_{Mt-1}	$\gamma/\alpha_t - 1$	$(\gamma - \alpha_t)/\alpha_t$	Whittaker's species turnover: effective species turnover expressed in multiples of the species diversity in a single compositional unit (measurement unit: $\mathrm{sp}_E/\mathrm{sp}_E$)
β_{Pt}	$1 - \alpha_t/\gamma$	$(\gamma - \alpha_t)/\gamma$	proportional species turnover: effective species turnover expressed as a proportion of total species diversity (measurement unit $\mathrm{sp}_E/\mathrm{sp}_E$)
H'_{β}	$H'_{\gamma} - H'_{\alpha}$	$\log({}^{1}\beta_{Md}) = \log(\gamma) - \log(\alpha_d)$	beta Shannon entropy (measurement unit: depends on the base of the logarithm)
$\bar{H}'_{\gamma-\gamma j}$	$H'_{\gamma} - \bar{H}'_{\gamma j}$	$\log({}^{1}\beta_{Mt}) = \log(\gamma) - \log(\alpha_t)$	regional Shannon entropy excess (measurement unit: depends on the base of the logarithm)
${}^{2}\bar{\lambda}_{\gamma j-\gamma}$	${}^{2}\bar{\lambda}_{\gamma j} - {}^{2}\lambda_{\gamma}$	$(\gamma - \alpha_t)/\gamma\alpha_t$	regional variance excess (measurement unit: $\mathrm{sp}_E/\mathrm{sp}_E^2$)

Shannon entropy H'_γ (also known as the Shannon index or Shannon-Wiener index) equals $\log({}^1D_\gamma)$ (Mathematical Proof 1). The $(1-q)$th root of ${}^q\lambda$ equals true diversity ${}^qD$, which is also known as Hill's (diversity) number or the numbers equivalent of the corresponding diversity index (Hill 1973, Peet 1974, Routledge 1979, Ricotta 2005, Jost 2006, 2007, Gregorius and Gillet 2008). All diversity indices based on ${}^q\lambda$ with the same value of q have the same numbers equivalent (Hill 1973, Jost 2006, 2007).

Hill (1973), Routledge (1979) and Jost (2006, 2007) made a strong case for quantifying diversity using ${}^qD$ rather than ${}^q\lambda$ or any of its transformations other than ${}^q\lambda^{1/(1-q)}$. With all values of q, true gamma diversity ${}^qD_\gamma$ is positively correlated with the number of actual species S and has the doubling property. This gives it a uniform and intuitive interpretation. In contrast, the interpretation of ${}^q\lambda_\gamma$ changes with the value of q: when $q<1$, ${}^q\lambda_\gamma$ is positively correlated with S whereas when $q>1$, ${}^q\lambda_\gamma$ is negatively correlated with S. When $q=1$, ${}^1\lambda_\gamma = \Sigma_{i=1}^{S} p_i$ equals unity by definition, whatever the values of S and p_i, so the Shannon entropy needs to be used instead if a diversity index with $q=1$ is desired. Furthermore, ${}^q\lambda_\gamma$ has the doubling property only when $q=0$, which easily leads to misinterpeting differences in ${}^q\lambda_\gamma$ when $q>0$ (Jost 2006, 2007).

Given the advantages of ${}^qD_\gamma$, it is surprising how few ecological studies have used it when a diversity measure that takes species abundances into account is needed (but see MacArthur 1964, 1965, Schlacher et al. 1998, Gray 2000, Ellingsen 2001, 2002, Chandy et al. 2006, Economo and Keitt 2008). In the present review, the focus will be on true diversities ${}^qD$ and mean proportional abundances $\bar{p}_i$, because this simplifies the discussion on diversity considerably. Diversity indices derived from ${}^q\lambda$ will be mentioned only to make connections to earlier literature.

Diversity in relation to two classifications

In the previous section, the only classification of interest was the γ-classification (the classification of individuals, or other units of abundance, into species). All calculations were done using overall species proportional abundances p_i, as if the dataset were a single sampling unit and Table 1 consisted of a single row. Expanding that row into multiple rows in effect introduces a second classification of the observed entities, namely their classification into sampling units at a more local scale of observation. This classification is here called the *ω-classification* (omega-classification).

The proportional abundance of the ith species in the entire dataset is obtained as the sum of the p_{ij} values in the ith column, which can be rewritten as the weighted arithmetic mean of the corresponding proportional abundances within the N sampling units (Table 1):

$$p_i = \sum_{j=1}^{N} p_{ij} = \sum_{j=1}^{N} \frac{m_{ij}}{m} = \sum_{j=1}^{N} \frac{m_j}{m}\frac{m_{ij}}{m_j} = \sum_{j=1}^{N} (w_j p_{i|j})$$

Here $p_{i|j} = m_{ij}/m_j$ is the proportional abundance of species i within sampling unit j, and each $p_{i|j}$ value is weighted by the proportion of the total abundance contained in the corresponding sampling unit $w_j = m_j/m$. If the total abundance is evenly distributed among the sampling units, all w_j equal $1/N$ and the weighted mean simplifies to an unweighted mean. Using modified sampling unit weights $w_{j\text{new}}$ (such as $1/N$ when the w_j are not equal) leads to quantifying p_i in a new table in which the proportion of the total abundance contained in sampling unit j is $w_{j\text{new}}/w_j$ times that in the original table. Conceptually, this corresponds to stretching the absolute abundance observed in sampling unit j from m_j to $m_{j\text{new}}$ abundance units. For example, a single bird could be treated as either one or more individuals, depending on which sampling unit it was observed in. The potential difference in p_i (and hence in mean p_i and in gamma diversity) between the actual and modified dataset increases as the value of q and/or the deviation of the $w_{j\text{new}}/w_j$ ratios from unity increase.

Modifying sampling unit weights by stretching may be justified if the $w_{j\text{new}}$ values represent relative sampling effort as quantified, for example, by plot area or duration of observation period. The results need to be interpreted with caution, however, because in reality the number of species and their proportional abundances change with absolute observed abundance. Therefore, rarefaction to a new, smaller absolute abundance $m_{j\text{new}}$ is often a better approach to modifying sampling unit weights. This is especially the case when the questions at hand are such that the effect of, for example, variation in bird observability or plant stem density is considered noise rather than a phenomenon of interest. The difference in p_i between the actual and rarefied dataset increases as the value of q decreases and/or the differences between $m_{j\text{new}}$ and the corresponding m_j increase. Obviously, any conclusions about diversity depend on appropriate weighting of sampling units.

Mean species diversity within the sampling units, or *alpha diversity*, will often also be of interest. This is quantified by first taking the weighted generalised mean of all within-sampling unit species proportional abundances in the dataset

$$\bar{p}_{(i|j)\text{all}} = \sqrt[q-1]{\sum_{j=1}^{N}\sum_{i=1}^{S} p_{ij} p_{i|j}^{q-1}}$$

The nominal weight p_{ij} equals the proportion of the entire dataset that was contributed by the corresponding $p_{i|j}$ value. The inverse of $\bar{p}_{(i|j)\text{all}}$ quantifies within-sampling unit species diversity α.

The measurement unit of α depends on which classifications are relevant for the questions at hand, and this will be indicated by lowercase subscripts. If only the γ-classification is of interest, the measurement unit is sp_E and the annotation α_t is used (the subscript "t" refers to turnover; Sections 3–5). Because this actually quantifies mean gamma diversity within the sampling units, the annotation ${}^q\bar{D}_{\gamma j} = \bar{\gamma}_j$ can also be used, where subscript "j" specifies that gamma diversity is quantified at the extent of a single sampling unit rather than at the extent of the entire dataset. If both the γ-classification and the ω-classification are of interest, the measurement unit is sp_E/SU where SU stands for *sampling unit*. When gamma diversity is partitioned into alpha and beta components, conclusions will actually be made about *compositional units* (CU). These are obtained by classifying the observed S_E effective species evenly into N_CU virtual sampling units (= compositional units) such that

each compositional unit receives α_t effective species shared by no other compositional unit. The classification of effective species into compositional units will be referred to as the β-classification. Taking into account both the γ-classification and the β-classification gives the measurement unit sp_E/CU. This is the hallmark of true alpha diversity α_d ($=^qD_\alpha$), where subscript "d" refers to diversity. The numerical values of α_d and α_t are identical, and the unsubscripted notation α will be used to refer to both.

It is also possible to calculate α_t as the weighted generalised mean with exponent $1-q$ of the γ_j ($=^qD_{\gamma j}$) values (Proof 2). This corresponds to the arithmetic mean when $q=0$, the geometric mean when $q=1$ and the harmonic mean when $q=2$. Whenever mean species diversity within sampling units is mentioned in the present paper, the *mean* therefore refers to *the weighted generalised mean with exponent 1 −* q *and sampling unit weights equal to* w_j. The same mean can be obtained as the numbers equivalent of the weighted arithmetic mean of the basic sums $^q\lambda_{\gamma j}$ or (when $q=1$) Shannon entropies $H'_{\gamma j}$ (Proof 3).

Mean within-sampling unit species diversity α_t ($=\bar{\gamma}_j = {}^q\bar{D}_{\gamma j}$) can never be larger than gamma diversity of the entire dataset γ, with equality being attained when each species is found in all sampling units at a constant proportional abundance. How much smaller than γ the weighted mean $\bar{\gamma}_j$ is depends both on the γ_j values and on the effective sampling unit weights. As q increases, the nominal weights w_j lose importance in the generalised mean used to calculate $\bar{\gamma}_j$ and the sampling units with the smallest γ_j gain progressively more weight. When calculating γ, in contrast, the sampling unit weights are used in an arithmetic mean no matter what the value of q, and the effective weights therefore always equal the nominal weights. The effects of the nominal weights on γ and α are therefore different, except in two special cases: when all w_j are equal (in which case the weighted mean simplifies to the unweighted mean), and when $q=1$ (in which case the effective weights in the generalised mean equal the nominal weights by definition). In these special cases, α_t is restricted to the range $[\gamma/N, \gamma]$, where the minimum value is obtained when the N actual sampling units share no species. When the w_j vary and $q\neq 1$, N_{CU} can exceed N with some combinations of γ_j, w_j and q. If nominal weights other than the row totals w_j are used, $\bar{\gamma}_j$ will be quantified for a new dataset derived by modifying the observed abundance values.

Choosing to quantify α_d implies that the γ-classification is the primary classification of interest, and the ω-classification is used only to define the limits of the sampling units within which species diversity is quantified. An alternative approach is to consider both classifications equally interesting, and to treat them symmetrically (Routledge 1979, Jost 2007). Then a measure of mean diversity per sampling unit can be obtained by first calculating the total diversity in relation to the γ- and ω-classifications simultaneously ('γω'), and then dividing this by the total diversity in relation to the ω-classification (ω). The numerator is obtained as the inverse of the mean of all species proportional abundance values p_{ij} and the denominator as the inverse of the mean of the sampling unit weights w_j (Proof 4). Consequently, the ratio 'γω'/ω $=^qD_{\gamma\omega'/\omega}$ quantifies the effective number of species abundance values (virtual cells with mean p_{ij} in Table 1) per effective sampling unit (virtual rows with mean w_j in Table 1). Jost (2007) used $^qD_{\gamma\omega'/\omega}$ as a measure of "alpha diversity", so the annotation α_R will also be used here. The subscript "R" refers to a ratio of two true diversities, and uppercase indicates that α_R differs from α_t and α_d both in numerical value and in measurement unit.

Jost (2007) derived α_R by taking the numbers equivalent of the weighted arithmetic mean of the basic sums $^q\lambda_{\gamma j}$ or Shannon entropies $H'_{\gamma j}$, and then w_j^q values are used as weights, instead of w_j values as when calculating α_t (Proof 4). Consequently, α_R equals α_t when either all sampling units have equal weights or $q=1$. When $q=0$, α_R of the original dataset equals α_t of a new dataset derived by modifying the observed abundance values. $^qD_{\gamma\omega'/\omega}$ ($=\alpha_R$) may exceed γ with some combinations of p_{ij}, w_j and q but it has a minimum value of γ/N, which is reached when none of the sampling units share any species. If all w_j are the same or q equals zero or unity, α_R is constrained to the interval $[\gamma/N, \gamma]$.

With these basic concepts, we are ready to tackle the problem of "beta diversity".

1. True beta diversity $\beta_{Md}=\gamma/\alpha_d$ and regional-to-local diversity ratio $\beta_{Mt}=\gamma/\alpha_t$

The definitions

In his example 3, Whittaker (1960) introduced the equation $\beta=\gamma/\alpha$ as a quantitative definition of beta diversity. This corresponds to a multiplicative partitioning of total species diversity $\gamma=\alpha\beta_M$ where subscript "M" refers to multiplicative. β_M is independent of the species richness of the system, as can be verified by the thought experiment of splitting each species: both α and γ will double, but their ratio will remain unchanged. At first, Whittaker (1960) used raw values of a diversity index (Fisher's alpha), but later he realised that numbers equivalents of diversity indices should be used (Whittaker 1972). Otherwise the gamma and alpha components may lack the doubling property, which would make the beta component dependent on the species richness of the system.

Whittaker (1972) discussed both gamma diversity and alpha diversity in terms of species diversity, and hence calculated the ratio $\gamma/\alpha_t = {}^qD_\gamma/{}^q\bar{D}_{\gamma j} = N_{CU}$. The resulting beta component β_{Mt} ($=^q\beta_{Mt}$) quantifies *how many times as rich in effective species an entire dataset is than its constituent sampling units are on average*. Because species diversity in each compositional unit equals mean species diversity in the actual sampling units, β_{Mt} also quantifies *how many times as rich in effective species the dataset is than one of its constituent compositional units*. β_{Mt} can be called the *regional-to-local diversity ratio*; it is a unitless scalar that quantifies the ratio of gamma diversities at two different levels of observation.

Using true alpha diversity α_d instead of α_t gives true beta diversity $\beta_{Md}=^q\beta_{Md}=\gamma/\alpha_d$. True beta diversity quantifies *the number of compositional units in the dataset*. In the previous section, the classification of effective species into compositional units was defined as the β-classification, so true beta diversity also quantifies *the total diversity in the dataset in relation to the β-classification*. This shows that β_{Md} is a true diversity, which can be emphasised by using the

annotation ${}^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$. Its measurement unit is $sp_E/(sp_E/CU) = CU$.

Discussions about alpha, beta and gamma diversity have usually ignored measurement units, which has probably contributed to the confusion around the concepts. After all, the plain numbers 1, 2 and 3 are much more easily compared as if they quantified the same phenomenon than are values such as 1 CU, 2 sp_E and 3 bits. The difference between true beta diversity β_{Md} and regional-to-local diversity ratio β_{Mt} is subtle, as their numerical values are the same. However, the difference in measurement unit is conceptually important. Whittaker (1960) observed that "The same types of measurements may be applied to 'gamma' as to 'alpha' diversity; 'beta' diversity represents a different problem". Whittaker (1977) referred to α and γ as *inventory diversity* and to β as *differentiation diversity*, which has since become a common practice (Magurran 2004). Some researchers have even argued that beta diversity should not be called diversity at all (Lande 1996, Kiflawi and Spencer 2004, Gregorius and Gillet 2008). This statement is justified if "beta diversity" is defined in terms of the regional-to-local diversity ratio β_{Mt} or species turnover (to be discussed in Sections 3–5), which really are conceptually different from true alpha and gamma diversity. However, true beta diversity β_{Md} is the number of compositional units, which is diversity in the very same sense as is the number of effective species.

Indeed, α_d ($= {}^{q}D_{\alpha}$), β_{Md} ($= {}^{q}D_{\beta}$) and γ ($= {}^{q}D_{\gamma}$) differ only because they focus on different entities (individuals in α_d and γ vs. effective species in β_{Md}) or on quantifying the diversity of the types into which those entities are classified at a different level (in the entire dataset in β_{Md} and γ vs per compositional unit in α_d). This justifies singling β_{Md} out as the sole measure of true beta diversity, and recommending that all other definitions of "beta diversity" be called something else.

As we saw above, $\beta_{Mt} = N_{CU}$. The minimum value of N_{CU} equals unity, obtained when all sampling units have the same species in the same proportional abundances. The maximum value that N_{CU} can take depends on the effective sampling unit weights, which determine the minimum value of α in relation to γ (*Diversity in relation to two classifications*, above). The values that β_{Mt} and β_{Md} take when no sampling units share any species therefore depend on both the ω-classification and the γ-classification. When either all w_j are equal or $q = 1$, N_{CU} cannot exceed N which constrains β_{Mt} to the interval [1, N] and β_{Md} to the interval [1 CU, N CU]. These ranges depend only on the ω-classification.

The generic term *multiplicative beta component* (β_M) will here be used to refer to either β_{Md} or β_{Mt}. Increasing the value of q makes ${}^{q}\beta_M$ more sensitive to the variation among sampling units in the proportional abundances of species and less sensitive to variation in species composition. Consequently, ${}^{0}\beta_M$ is not affected by changes in species abundances (as long as presence-absence patterns do not change), and ${}^{\infty}\beta_M$ is not affected by changes in species composition (as long as the abundance of the single most abundant species does not change).

It is important to notice that the logical consistency of β_M necessitates that both γ and α are based on the same dataset. This implies that the weight given to sampling unit j has to be the same when calculating γ and when calculating α. Using the row totals from Table 1 as sampling unit weights gives the alpha, beta and gamma diversities of that table. Using some other weights gives the diversity components of a new table in which observed abundances have been modified according to the weights. If different weights are used when calculating γ and when calculating α, these will be quantified for different datasets. Dividing γ of one dataset by α of another dataset produces a ratio that does not correspond to β_M for either dataset.

If each sampling unit represents a community (or a habitat) and all sampling units together represent a region, true beta diversity represents the number of compositionally non-overlapping community (or habitat) types in the region. This interpretation is ecologically accurate only if each sampling unit is sufficiently large to be truly representative of its community (or habitat), and if enough sampling units have been inventoried for them to be truly representative of the entire region. In practical applications these conditions are seldom met, but evaluating how sampling problems may affect the reliability of extrapolations beyond the dataset at hand is deferred to the second part of the present review (Tuomisto 2010).

β_M, especially as applied to presence-absence data, is one of the most popular definitions of "beta diversity" in ecology (Routledge 1977, 1979, Lee and La Roi 1979, McCune and Antos 1981, Stoms 1994, Weiher and Boylen 1994, Gray 2000, Perelman et al. 2001, Vellend 2001, Arita and Rodríguez 2002, Ellingsen and Gray 2002, Harrison and Inoye 2002, Rodríguez and Arita 2004, Wiersma and Urban 2005, Lira-Noriega et al. 2007, Passy and Blanchet 2007, Arita et al. 2008, Gallardo-Cruz et al. 2009). Some of these studies clearly discussed true beta diversity β_{Md} and others regional-to-local diversity ratio β_{Mt}, but not all specified their interpretation.

Hierarchical diversity partitioning

Above, true gamma diversity was partitioned into two independent components. If the γ- or ω-classifications are hierarchically structured, more than two independent components can be obtained. Hierarchical ω-classification means that each row in Table 1 represents data that have been pooled from a number of smaller sampling units, possibly over several hierarchical levels. Let us identify the hierarchical levels such that the highest hierarchical level below that of the entire dataset is level 1, the next more local level is level 2, and so on. If the number of level-1 sampling units is N_1 and the number of level-2 sampling units is N_2, Table 1 could contain either N_1 or N_2 rows, depending on which level is shown. The cell values would then be adapted accordingly, such that the p_{ij} values in a given level-1 sampling unit are the species-wise sums of the p_{ij} values in its constituent level-2 sampling units. Partitioning gamma diversity (species diversity in the entire dataset) at level 1 gives the true diversity components α_1 (mean species diversity per level-1 compositional unit) and β_1 (effective number of level-1 compositional units in the entire dataset). Level-1 alpha diversity can be further partitioned into the true diversity components α_2 (mean species diversity per level-2 compositional unit) and $\sigma_{2/1}$

(mean level-2 compositional unit diversity per level-1 compositional unit). Similarly, α_2 can be partitioned into α_3 and $\sigma_{3/2}$ and so on.

The new diversity component σ (sigma) is analogous to α because it is quantified as a mean of diversities observed per compositional unit, rather than as a single value for the entire dataset. The relationship between beta diversity and sigma diversity is therefore similar to that between gamma diversity and alpha diversity. The measurement unit of γ is sp_E and that of α_h is sp_E/CU_h where CU_h stands for level-h compositional unit. Analogously, the measurement unit of β_1 is CU_1 and that of $\sigma_{(h+1)/h}$ is CU_{h+1}/CU_h.

These true diversities are multiplicatively related by

$$\gamma = \alpha_3\sigma_{3/2}\sigma_{2/1}\beta_1$$

The units of measurement on the right side of this equation are

$$(sp_E/CU_3)(CU_3/CU_2)(CU_2/CU_1)CU_1 = sp_E$$

as we would expect of gamma diversity.

Gamma diversity can be partitioned at any hierarchical level into alpha and beta diversities at the same level, or alpha and beta diversities at different levels complemented by sigma diversity of appropriate level(s). For example,

$$\gamma = \alpha_2\beta_2 \text{ where } \alpha_2 = \alpha_3\sigma_{3/2} \text{ and } \beta_2 = \sigma_{2/1}\beta_1$$

A hierarchically structured γ-classification can be used in a similar way. This allows quantifying what proportion of the observed total species diversity is due to, for example, species diversity within genera, genus diversity within families and so on (Pielou 1975, pp. 17–18).

Heterogeneity measures

Recently, Jurasinski et al. (2009) argued that there is a conceptual difference between beta diversity as calculated from the relationship between alpha and gamma diversity, and beta diversity as quantified using distance coefficients. In fact, many (dis)similarity coefficients can be derived from alpha and gamma diversity as calculated for a dataset that consists of two sampling units. Different definitions of "beta diversity" therefore naturally give rise to different dissimilarity coefficients.

MacArthur (1965) measured the faunal difference between two censuses by $\exp(H'_{obs} - H'_{min})$. In the annotation of the present paper, MacArthur's measure equals

$$\exp(H'_\gamma - \bar{H}'_{\gamma j}) = \exp(\log(\gamma) - \log(\alpha_t)) = \gamma/\alpha_t = {}^1\beta_{Mt}$$

More generally, ${}^q\beta_M$ can be used as an index of total compositional heterogeneity in a dataset at the scale represented by the sampling units. However, ${}^q\beta_M$ does not measure compositional heterogeneity among the sampling units themselves. This is because it can obtain the same value with a small number of compositionally dissimilar samping units or with a larger number of more similar sampling units. If compositional heterogeneity among sampling units is of interest, ${}^q\beta_M$ can be partitioned into two independent components:

$${}^q\beta_{Mt} = \frac{{}^q\beta_{Mt}}{N}N = \frac{N_{CU}}{N}N$$

N_{CU}/N quantifies mean heterogeneity per sampling unit, i.e. how many compositional units there are for each actual sampling unit in the dataset. If all sampling units have the same weight or $q = 1$, ${}^q\beta_{Mt}$ is constrained to values in the interval $[1, N]$ and N_{CU}/N becomes constrained to $[1/N, 1]$.

When ${}^q\beta_{Mt}$ is calculated for two sampling units ($N = 2$) using presence-absence data ($q = 0$) and equal sampling unit weights, it is inversely related with the Jaccard index (C_J) and linearly (and negatively) related with the Sørensen index (C_S). In the equations below (and in others that will follow), a is the number of species shared by both sampling units, b is the number of species unique to the first sampling unit and c is the number of species unique to the second sampling unit.

$$\begin{aligned}
{}^0\beta_{Mt} &= \frac{\gamma}{\alpha_t} = \frac{a+b+c}{[(a+b)+(a+c)]/2} = \frac{2(a+b+c)}{2a+b+c} \\
&= 2\Big/\left(\frac{2a+b+c}{a+b+c}\right) = 2\Big/\left(1+\frac{a}{a+b+c}\right) \\
&= \frac{2}{1+C_J}
\end{aligned}$$

$$\begin{aligned}
{}^0\beta_{Mt} &= \frac{\gamma}{\alpha_t} = \frac{a+b+c}{[(a+b)+(a+c)]/2} = \frac{2a+2b+2c}{2a+b+c} \\
&= \frac{4a+2b+2c}{2a+b+c} - \frac{2a}{2a+b+c} = 2 - \frac{2a}{2a+b+c} \\
&= 2 - C_S
\end{aligned}$$

Although both the Jaccard and the Sørensen index are monotonic transformations of ${}^0\beta_M$, they are still transformations and therefore do not quantify either ${}^0\beta_{Mt}$ or ${}^0\beta_{Md}$. It is also important to keep in mind that the relevant ${}^0\beta_M$ here is that of two equally weighted sampling units (*Diversity in relation to two classifications*, above).

2. Two-way diversity ratio $\beta_R = \gamma/\alpha_R$

Jost (2007) required that in addition to being independent of alpha diversity, beta diversity should be monotonic with respect to compositional differentiation among the sampling units (given the ω-classification). This led him to divide gamma diversity by the effective number of species abundance values per effective sampling unit ($\alpha_R = {}^qD_{\gamma\omega'/\omega}$; *Diversity in relation to two classifications*, above). Jost's definition of "beta diversity" is therefore ${}^q\beta_R = \gamma/\alpha_R$ which equals

$${}^qD_{\gamma\omega/'\gamma\omega'} = \frac{{}^qD_\gamma}{{}^qD_{\gamma\omega'}/{}^qD_\omega} = \frac{{}^qD_\gamma\,{}^qD_\omega}{{}^qD_{\gamma\omega'}} = \left(\frac{\bar{p}_i\bar{w}_j}{\bar{p}_{ij}}\right)^{-1}$$

The numerator equals the number of effective species (= number of virtual columns with mean p_i in Table 1) multiplied by the number of effective sampling units (= number of virtual rows with mean w_j). The denominator equals the number of effective species–sampling unit combinations (= number of virtual cells with mean p_{ij}). Jost (2007) showed that ${}^qD_{\gamma\omega/'\gamma\omega'}$ is monotonically related with compositional differentiation among sampling units only when either all sampling unit weights w_j are equal or

q equals zero or unity, and therefore restricted its use to these special cases.

However, ${}^{q}D_{\gamma\omega/'\gamma\omega'}$ has a logical interpretation in terms of diversity with any w_j and q values. It quantifies *how many times as much diversity in relation to the γ- and ω-classifications there is in the dataset when the classifications are considered separately vs when they are considered together.* ${}^{q}D_{\gamma\omega/'\gamma\omega'} = {}^{q}\beta_{R}$ can be called *two-way diversity ratio*, since it compares diversities in relation to two different classifications, calculated in two different ways. The logical measurement unit of both the numerator and the denominator is $sp_{E}SU_{E}$ (the product of effective species and effective sampling units), so ${}^{q}\beta_{R}$ simplifies to a unitless scalar. It has a maximum value of N, which is obtained when no sampling units share species, but no fixed lower limit except in the special cases when it is monotonically related with differentiation. Then the minimum value is unity, which is obtained when all sampling units have the same species in the same proportional abundances. When all sampling unit weights are equal or $q = 1$, ${}^{q}\beta_{R}$ equals regional-to-local diversity ratio ${}^{q}\beta_{Mt}$. When $q = 0$, ${}^{q}\beta_{R}$ of the original dataset equals ${}^{q}\beta_{Mt}$ of a new dataset in which the abundances observed in all sampling units have been modified so as to be equal.

3. Regional diversity excess (absolute effective species turnover) $\beta_{At} = \gamma - \alpha_{t}$

Regional diversity excess β_{At} (or ${}^{q}\beta_{At}$) corresponds to additive partitioning of total diversity $\gamma = \alpha + \beta$ and equals $\beta_{At} = \gamma - \alpha_{t} = {}^{q}D_{\gamma} - {}^{q}\bar{D}_{\gamma j}$ where subscript "A" indicates additive. This quantifies *the amount by which the effective species richness of the entire (regional) dataset exceeds that of a single sampling unit of mean effective species richness.*

Both $\alpha_{t} + \beta_{At}$ and $\alpha_{t}\beta_{Mt}$ equal gamma diversity, from which follows

$$\beta_{At} = \alpha_{t}\beta_{Mt} - \alpha_{t} = \alpha_{t}(\beta_{Mt} - 1) = \alpha_{t}(N_{CU} - 1)$$

All effective species not present in one compositional unit have to be present in the other $N_{CU} - 1$ compositional units, which causes turnover of effective species. Therefore, β_{At} can also be interpreted as *the absolute amount of effective species turnover among the compositional units of the dataset* (hence the subscript "t").

The minimum value of ${}^{q}\beta_{At}$ is zero effective species, which is obtained when all actual sampling units have the same species in constant proportional abundances. The maximum value depends on both the number of compositional units and on α_{t}. If either all sampling unit weights are equal or $q = 1$, then N_{CU} cannot exceed N and ${}^{q}\beta_{At}$ is constrained not to exceed $(N-1)\alpha_{t}$. In these special cases, ${}^{q}\beta_{At}$ also quantifies absolute effective species turnover among the N actual sampling units. If $q = 0$, effective species equal actual species, so if all sampling unit weights are equal then ${}^{0}\beta_{At}$ can also be interpreted as absolute actual species turnover among the N actual sampling units.

Because $\beta_{At} = \alpha_{t}(\beta_{Mt} - 1)$ and, equivalently, $\beta_{Mt} = \beta_{At}/\alpha_{t} + 1$, it is obvious that absolute effective species turnover β_{At} is not monotonically related with β_{Mt} and β_{Md} when the datasets to be compared differ in α. Whereas β_{M} is independent of the species diversity of the observed system, β_{At} is not. Consider the thought experiment of duplicating each species: not only α_{t} and γ will double, but β_{At} will also double. Therefore, absolute effective species turnover may be smaller in a species-poor region with many compositional units than in a species-rich region with few compositional units, and conflicting results may be obtained if regional datasets are ranked on the basis of both β_{At} and β_{M}.

When calculated for two sampling units with $q = 0$ and equal sampling unit weights, absolute effective species turnover is related to the Manhattan metric (M) and the Euclidean distance (E) as calculated using presence-absence data (a, b, and c as in Section 1):

$${}^{0}\beta_{At} = \gamma - \alpha_{t} = a + b + c - \frac{a + b + a + c}{2} = \frac{b + c}{2}$$

$$= \frac{1}{2}\sum_{i=1}^{S} |m_{i1} - m_{i2}| = \frac{1}{2}M$$

$${}^{0}\beta_{At} = \frac{b + c}{2} = \frac{1}{2}\sum_{i=1}^{S} (m_{i1} - m_{i2})^{2} = \frac{1}{2}E^{2}$$

In these equations, m_{i1} is the abundance of species i in the first sampling unit and m_{i2} in the second (the abundance data have to be binary: 0 for absence, 1 for presence). Absolute effective species turnover can therefore be used to generalise either the Manhattan metric or the squared Euclidean distance to a presence-absence dataset with multiple equally-weighted sampling units. Both dissimilarity indices have properties that are not desirable when applied to compositional data (Legendre and Legendre 1998), so they have not been particularly popular in beta diversity studies (but see Weiher and Boylen 1994, Schlacher et al. 1998, Koleff et al. 2003b).

MacArthur (1964, 1965) seems to have been the first one to partition species diversity data using an additive equation, but he restricted its use to the Shannon entropy. The additive equation

$$H'_{\gamma} = H'_{\alpha} + H'_{\beta}$$

can be rewritten

$$\exp(H'_{\gamma}) = \exp(H'_{\alpha} + H'_{\beta})$$
$$= \exp(H'_{\alpha})\exp(H'_{\beta})$$

which equals (Proof 1)

$${}^{1}D_{\gamma} = {}^{1}D_{\alpha}\,{}^{1}D_{\beta}$$

Both MacArthur (1965) and Routledge (1977, 1979) observed that converting Shannon entropies to their numbers equivalents leads to Whittaker's multiplicative diversity components. This relationship has been discussed several times recently (Ricotta 2005, Jost 2006, 2007).

Although it is possible to rephrase

$${}^{1}D_{\gamma} = {}^{1}D_{\alpha}\,{}^{1}D_{\beta} \Leftrightarrow H'_{\gamma} = {}^{q}H'_{\alpha} + {}^{q}H'_{\beta} \quad \text{to read}$$
$$\gamma = \alpha\beta \Leftrightarrow \gamma' = \alpha' + \beta'$$

this easily leads to confusing true diversities with indices of diversity, and to applying the additive partitioning to diversity indices for which a beta component that is independent on the species richness of the system cannot

be obtained (see also Jost 2007). In the present paper, the symbols α, β and γ are used only when referring to the components of true diversity, and the symbols α', β' and γ' when referring to raw diversity index values.

Regional diversity excess β_{At} was hardly used until Lande (1996) and Veech et al. (2002) argued that measuring alpha and beta "diversity" in the same units (in this case, sp or sp_E) is an advantage. Lande (1996) followed Nei (1973) and Patil and Taillie (1982) in applying the additive partitioning $\gamma' = \alpha' + \beta'$ not only to the Shannon entropy but also to other diversity indices such as ${}^0\lambda$. Because ${}^0\lambda = {}^0D$, this leads to an additive rather than multiplicative partitioning of true gamma diversity, and the meaning of the beta component is thereby changed. Regional diversity excess β_{At} has become a popular measure of "beta diversity", especially when partitioning regional species richness at multiple spatial scales (Wagner et al. 2000, Gering and Crist 2002, Crist et al. 2003, Gering et al. 2003, Summerville et al. 2003, Roschewitz et al. 2005, Chandy et al. 2006, Crist and Veech 2006, Freestone and Inouye 2006, Tylianakis et al. 2006, Belmaker et al. 2008, Chiarucchi et al. 2008, Gardezi and Gonzalez 2008, Klimek et al. 2008, Ribeiro et al. 2008, Sobek et al. 2009).

Regional diversity excess has been referred to as "additive beta diversity" (Kiflawi and Spencer 2004, Ricotta 2005, 2008, Economo and Keitt 2008), but it is conceptually very different from true beta diversity. Whereas β_{Md} is a true diversity (=effective number of types), β_{At} is not. Instead, β_{At} quantifies the difference in true species diversity between the entire dataset and an average sampling unit. Using the generic term beta diversity to refer to both phenomena leads to confusion and should be avoided. It is also important to distinguish absolute effective species turnover from relative effective species turnover, which will be discussed next.

4. Effective species turnover expressed in multiples of mean species diversity of a single sampling unit (Whittaker's effective species turnover) $\beta_{Mt-1} = (\gamma - \alpha_t)/\alpha_t$

Regional-to-local diversity ratio β_{Mt} obtains its minimum value of unity when all sampling units are compositionally identical and there is no species turnover among them. Whittaker (1972) developed from β_{Mt} a species turnover measure with a minimum value of zero that quantifies *the number of complete effective species turnovers among compositional units in the dataset* and equals

$$\beta_{Mt-1} = \beta_{Mt} - 1 = \gamma/\alpha_t - 1 = {}^qD_\gamma / {}^q\bar{D}_{\gamma j} - 1$$

Rephrasing this equation gives $\beta_{Mt-1} = (\gamma - \alpha_t)/\alpha_t = \beta_{At}/\alpha_t$, which shows that β_{Mt-1} simply relates absolute effective species turnover to mean species diversity of the sampling units. Equivalently, $\beta_{At} = \alpha_t \beta_{Mt-1}$ (see also Kiflawi and Spencer 2004; note that β_M refers to both β_{Mt} and β_{Mt-1} in their text). In other words, β_{Mt-1} expresses *effective species turnover among the compositional units of the dataset in multiples of their effective species richness*. Unlike β_{At}, β_{Mt-1} is independent of the species richness of the system, so the two are not monotonically related when the datasets to be compared differ in α_t. Absolute and relative effective species turnover can therefore lead to different rankings of datasets.

Given that both β_{Mt} and β_{Mt-1} were proposed by Whittaker (1960, 1972), it is not surprising that both have been referred to as "Whittaker's beta diversity". However, β_{Mt-1} quantifies a specific kind of species turnover rather than a true diversity, so it is better referred to as *Whittaker's (effective) species turnover*. Nevertheless, β_{Mt-1} has been used as a measure of "beta diversity" in several papers (Wilson and Shmida 1984, Blackburn and Gaston 1996, Davis et al. 1999, Clarke and Lidgard 2000, Ellingsen 2001, 2002, Koleff and Gaston 2001, Sweeney and Cook 2001, Davis 2005, Mena and Vázquez-Domínguez 2005, Munari and Mistri 2008).

When calculated for two sampling units using species richness ($q = 0$) and equal sampling unit weights, Whittaker's species turnover is linearly (and negatively) related with the Sørensen index (C_S):

$${}^0\beta_{Mt-1} = {}^0\beta_{Mt} - 1 = (2 - C_S) - 1 = 1 - C_S$$

Consequently, all studies that aimed to quantify "beta diversity" and chose the one-complement of the Sørensen index to do so actually quantified Whittaker's species turnover (Vazquez and Givnish 1998, Price et al. 1999, Condit et al. 2002, Wiersma and Urban 2005, Graham et al. 2006, Normand et al. 2006, Ødegaard 2006, Novotny et al. 2007, Ruokolainen et al. 2007, Hernández et al. 2008, Klop and Prins 2008, Linares-Palomino and Kessler 2009).

If either all sampling unit weights are equal or $q = 1$, Whittaker's effective species turnover obtains a maximum value of $N-1$ when the N sampling units share no species. Then β_{Mt-1} can be ranged to the interval [0, 1]:

$$\begin{aligned} {}^q\hat{\beta}_{Mt-1} &= \frac{{}^q\beta_{Mt-1} - {}^q\beta_{Mt-1min}}{{}^q\beta_{Mt-1max} - {}^q\beta_{Mt-1min}} = \frac{{}^q\beta_{Mt-1} - 0}{(N-1) - 0} \\ &= \frac{{}^q\beta_{Mt-1}}{N-1} = \frac{{}^q\beta_{Mt} - 1}{N-1} = {}^q\hat{\beta}_{Mt} \end{aligned}$$

Here "min" and "max" refer to the minimum and maximum values, respectively, that can be obtained given the number of sampling units N. Ranging Whittaker's effective species turnover and ranging regional-to-local diversity ratio lead to exactly the same result, because the two are linearly related. Since the ranged index is constrained to a fixed maximum value irrespective of N, it does not quantify Whittaker's effective species turnover even though it is based on it. Instead, ${}^q\hat{\beta}_{Mt-1}$ quantifies the amount by which β_{Mt-1} exceeds its minimum possible value, expressed as a proportion of the total possible range of values (given N and the constraint of equal sampling unit weights when $q \neq 1$). For $q = 0$, the ranged index has been proposed by Harrison et al. (1992), who called it beta-1. ${}^q\hat{\beta}_{Mt-1}$ can be interpreted in terms of compositional differentiation among the N sampling units, so its one-complement is a measure of compositional overlap:

$$\begin{aligned} 1 - {}^q\hat{\beta}_{Mt-1} &= 1 - {}^q\hat{\beta}_{Mt} = \frac{N-1}{N-1} - \frac{{}^q\beta_{Mt} - 1}{N-1} \\ &= \frac{N - {}^q\beta_{Mt}}{N-1} = {}^qC_{SN} \end{aligned}$$

When $q=0$ and $N=2$, ${}^{q}C_{SN}$ simplifies to the Sørensen index. In a dataset with more than two sampling units, pairwise Sørensen index values are not sensitive to whether or not some species are shared by three or more sampling units, but Whittaker's effective species turnover, its ranged version and ${}^{q}C_{SN}$ are. The Sørensen index has been generalised to N sampling units by Diserud and Ødegaard (2007), who derived the ranging equation shown above for ${}^{0}C_{SN}$. Jost (2006) derived a pairwise overlap measure for any value of q by ranging a monotonic transformation of ${}^{q}\beta_{Mt}$, and Chao et al. (2008) generalised it to $N \geq 2$ sampling units. This generalised index, C_{qN}, also yields the Sørensen index as a special case when $q=0$ and $N=2$. With other values of q, C_{qN} and ${}^{q}C_{SN}$ behave in different ways, as will be seen presently.

Both Whittaker's species turnover ${}^{q}\beta_{Mt-1}$ and its ranged version ${}^{q}\hat{\beta}_{Mt-1}$ depend on N, but in different ways (the same is true of ${}^{q}\beta_{Mt}$ and ${}^{q}\hat{\beta}_{Mt}$). This is easiest to visualise for $q=0$, equal sampling unit weights and constant ${}^{0}D_{\gamma j}$. When N increases, ${}^{0}\beta_{Mt-1}$ remains constant if the new sampling units do not introduce any new species to the dataset. Average compositional overlap among the sampling units then has to increase (unless they were identical to start with), and ${}^{0}\hat{\beta}_{Mt-1}$ has to decrease (the numerator remains constant while the denominator increases). Conversely, ${}^{0}\hat{\beta}_{Mt-1}$ remains constant if the newly added sampling units have the same average overlap with the original set of sampling units as these previously had among themselves. This is possible only if the new sampling units do introduce some new species to the dataset, in which case ${}^{0}\beta_{Mt-1}$ necessarily increases. In general, ${}^{q}\beta_{Mt-1}$ and ${}^{q}\hat{\beta}_{Mt-1}$ are linearly related when N is constant, but the correlation between them grows weaker with increasing variation in N. Consequently, the two do not measure the same phenomenon and can rank datasets differently.

5. Effective species turnover expressed as a proportion of total species diversity (proportional effective species turnover) $\beta_{Pt}=(\gamma-\alpha_t)/\gamma$

To obtain Whittaker's effective species turnover, absolute effective species turnover β_{At} is divided by the mean species diversity of the compositional units. Equally well, β_{At} can be divided by total species diversity. Doing so leads to a new kind of relative effective species turnover measure, namely $\beta_{Pt}=(\gamma-\alpha_t)/\gamma$. The equation can be rephrased $\beta_{Pt}=1-\alpha_t/\gamma=1-{}^{q}\bar{D}_{\gamma j}/{}^{q}D_{\gamma}$. This quantifies *the proportion of the effective species of the entire dataset that is not contained in a single compositional unit*. When $q=0$ and all sampling unit weights are equal, the term $\alpha_t/\gamma=1/\beta_{Mt}$ also indicates the proportion of sampling units in which the average species occurs (mean species frequency; Whittaker 1972, Routledge 1977, Arita et al. 2008).

The relationship between the diversity components can also be written $\gamma=\alpha_t/(1-\beta_{Pt})$ where the subscript "P" refers to a proportional partitioning of gamma diversity. From the above equations it follows that $\beta_{Pt}=1-1/\beta_{Mt}=\beta_{Mt-1}/\beta_{Mt}$ or equivalently $\beta_{Mt}=1/(1-1/\beta_{Pt})$. Furthermore, $\beta_{Pt}=\beta_{At}/\gamma$ or equivalently $\beta_{At}=\gamma\beta_{Pt}$. Proportional effective species turnover β_{Pt} is independent of the species richness of the system, so it may give results that are in conflict with those obtained with absolute effective species turnover β_{At} if the datasets to be compared differ in gamma diversity. In contrast, β_{Pt}, β_{Mt-1}, β_{Mt} and β_{Md} are monotonically related to each other. Consequently, if one wishes to rank datasets on the basis of their relative effective species turnover or multiplicative beta component, identical results will be obtained. However, the relationship between the proportional and multiplicative measures is not linear.

When calculated for two sampling units using species richness ($q=0$) and equal weights, ${}^{q}\beta_{Pt}$ is linearly (and negatively) related with the Jaccard index and inversely related with the Sørensen index:

$${}^{0}\beta_{Pt}=1-\frac{1}{{}^{0}\beta_{Mt}}=1-\frac{1+C_J}{2}=\frac{1-C_J}{2}$$

$${}^{0}\beta_{Pt}=1-\frac{1}{{}^{0}\beta_{Mt}}=1-\frac{1}{2-C_S}$$

The Jaccard index can hence be expressed $C_J=1-2({}^{0}\beta_{Pt})$. By allowing q to vary, the general similarity index ${}^{q}C_J=1-2({}^{q}\beta_{Pt})$ is obtained, which can also be expressed ${}^{q}C_J=2/{}^{q}\beta_{Mt}-1$. The minimum value of β_{Pt} is zero, which is obtained when all sampling units have the same species in constant proportional abundances. When all sampling units have the same weight or $q=1$, β_{Pt} is constrained not to exceed $1-1/N$, with this maximum being obtained when none of the N sampling units share any species. Then ${}^{q}\beta_{Pt}$ can be ranged to the interval [0, 1] by the equation

$${}^{q}\hat{\beta}_{Pt}=\frac{{}^{q}\beta_{Pt}-{}^{q}\beta_{Ptmin}}{{}^{q}\beta_{Ptmax}-{}^{q}\beta_{Ptmin}}=\frac{{}^{q}\beta_{Pt}}{1-1/N}=\frac{1-1/{}^{q}\beta_{Mt}}{1-1/N}$$

The one-complement of this ranged index is

$$\begin{aligned}1-{}^{q}\hat{\beta}_{Pt}&=1-\frac{{}^{q}\beta_{Pt}}{1-1/N}=\frac{1-1/N-{}^{q}\beta_{Pt}}{1-1/N}\\&=\frac{1-1/N-(1-1/{}^{q}\beta_{Mt})}{1-1/N}=\frac{1/{}^{q}\beta_{Mt}-1/N}{1-1/N}\\&={}^{q}C_{JN}\end{aligned}$$

where ${}^{q}C_{JN}$ is the generalisation of the Jaccard index to any value of q and any number of sampling units (under the constraint of equal sampling unit weights when $q\neq 1$). ${}^{q}C_{JN}$ simplifies to the classic Jaccard index when $q=0$ and $N=2$. The index of biotal dispersity proposed by Koch (1957) equals ${}^{0}C_{JN}$. The general ranging equation for ${}^{q}C_{JN}$ was derived by Jost (2006), who showed that for $N=2$ and $q=2$ it equals the Morisita-Horn index. The C_{qN} measure of Chao et al. (2008) also yields ${}^{2}C_{JN}$ at $q=2$, but as we saw in Section 4, at $q=0$ it equals ${}^{0}C_{SN}$ instead. As always, ranging changes the numerical values such that the ecological interpretation of the ranged index (${}^{q}C_{JN}$) is not the same as that of the original measure ($1-{}^{q}\beta_{Pt}$ or $1/{}^{q}\beta_{Mt}$).

Because example 1 of Whittaker (1960) applied the Jaccard index, it was in fact based on ranged values of proportional species turnover rather than on true beta diversity. Many other studies have followed suit, as the Jaccard index (or its one-complement, also known as the

complementarity of Colwell and Coddington 1994) has been a popular measure of "beta diversity" (Scheiner and Rey-Benayas 1994, Rey Benayas 1995, Porembski et al. 1996, Harrison 1997, Clarke and Lidgard 2000, Izsak and Price 2001, Pärtel et al. 2001, Balvanera et al. 2002, Tuomisto et al. 2003, Tuomisto and Ruokolainen 2005, Chust et al. 2006, Freestone and Inouye 2006, Harrison et al. 2006, Ødegaard 2006, Flores-Palacios and García-Franco 2008).

Roschewitz et al. (2005) presented ${}^{0}\beta_{Pt}$ values under the name "relative beta diversity", which they derived using the additive partitioning of total species richness as a starting point. Several other authors have also noticed that dividing "additive beta diversity" ${}^{0}\beta_{At}$ by gamma diversity makes the beta component independent of alpha diversity, and consequently presented proportional species turnover values as "additive beta diversity" values (Crist and Veech 2006, Veech and Crist 2007, Hof et al. 2008, Ricotta 2008).

6. Beta Shannon entropy $H'_\beta = H'_\gamma - H'_\alpha$ and regional Shannon entropy excess $\bar{H}'_{\gamma-\gamma j} = H'_\gamma - \bar{H}'_{\gamma j}$

As we saw in Section 3 (*Regional diversity excess*), multiplicative partitioning of true diversities of order 1 (${}^{1}D_\gamma = {}^{1}D_\alpha \, {}^{1}D_\beta$) corresponds to additive partitioning of Shannon entropies ($H'_\gamma = H'_\alpha + H'_\beta$). Using the beta component of the Shannon entropy without converting it to its numbers equivalent ${}^{1}D_\beta$ leads to a new definition of "beta diversity", namely $H'_\beta = H'_\gamma - H'_\alpha = \log({}^{1}D_\beta) = \log({}^{1}\beta_{Md})$. Here H'_γ is Shannon entropy related to the γ-classification, H'_α is Shannon entropy related to the γ-classification that is conditional on the β-classification, and H'_β is Shannon entropy related to the β-classification. In other words, H'_γ quantifes the mean uncertainty regarding which effective species is picked when one individual (or other unit of abundance) is taken at random from the entire dataset. H'_α quantifes the mean uncertainty regarding which effective species is picked when one individual (or other unit of abundance) is taken at random from the entire dataset, but the uncertainty is quantified only within the limits of the compositional unit that contains the effective species to which the chosen individual belongs. Beta Shannon entropy H'_β quantifies *the uncertainty regarding which compositional unit is picked when one effective species is taken at random from the entire dataset*.

The Shannon entropy corresponding to mean species diversity in the sampling units $\log(\alpha_\tau) = \log({}^{1}\bar{D}_{\gamma j}) = \bar{H}'_{\gamma j}$ quantifies the mean uncertainty regarding which effective species is picked when one individual (or other unit of abundance) is taken at random from within a randomly preselected sampling unit. If $\bar{H}'_{\gamma j}$ is used instead of H'_α when partitioning gamma Shannon entropy, the beta component becomes regional Shannon entropy excess $\bar{H}'_{\gamma-\gamma j} = H'_\gamma - \bar{H}'_{\gamma j} = \log({}^{1}\beta_{Mt})$. This quantifies *the amount by which the Shannon entropy of the regional dataset (in relation to the γ-classification) exceeds that of a single sampling unit of arithmetic mean entropy*. Although the interpretations of H'_β and $\bar{H}'_{\gamma-\gamma j}$ are different, their numerical values are the same.

The minimum value of both H'_β and $\bar{H}'_{\gamma-\gamma j}$ is zero, which is obtained when there is no variation in species proportional abundances among sampling units. The maximum value is $\log(N)$ for $\bar{H}'_{\gamma-\gamma j}$ and $\log(N \text{ CU})$ for H'_β, which are obtained when none of the N sampling units share any species. Depending on which base is chosen for the logarithm, H'_β and $\bar{H}'_{\gamma-\gamma j}$ are measured in different units, such as bits, nats or decits (Shannon 1948; Proof 1).

Although Shannon entropy related to the β-classification and regional Shannon entropy excess are monotonic transformations of true beta diversity ${}^{1}\beta_{Md}$, they do not equal true beta diversity. The relationship is strongly curvilinear, because the logarithm of a variable increases much more slowly than the variable itself. This can easily lead to errors of interpretation if entropy is confused with true diversity (see Jost 2006, 2007 for further discussion). Nevertheless, it has been rather common in the ecological literature to use H'_β or $\bar{H}'_{\gamma-\gamma j}$ as a measure of "beta diversity" (Levins 1968, Allan 1975a, b, Holland and Jain 1981, Barker et al. 1983, Gimaret-Carpentier et al. 1998, Wagner et al. 2000, Crist et al. 2003, Gering et al. 2003, Summerville et al. 2003, Couteron and Pélissier 2004, Pélissier and Couteron 2007, Basset et al. 2008).

Horn (1966) developed the following indices on the basis of Shannon entropies:

$$R_o = \frac{H'_{\max} - H'_{\text{obs}}}{H'_{\max} - H'_{\min}} = 1 - \frac{H'_{obs} - H'_{\min}}{H'_{\max} - H'_{\min}} = 1 - R_h$$

R_o stands for an overlap index and R_h for the corresponding heterogeneity index. In the annotation of the present paper, Horn's heterogeneity index can be rewritten

$$R_h = \frac{H'_\gamma - \bar{H}'_{\gamma j}}{H'_{\gamma\max} - \bar{H}'_{\gamma j}} = \frac{\log(\gamma) - \log(\alpha_\tau)}{\log(2\alpha_\tau) - \log(\alpha_\tau)} = \frac{\log({}^{1}\beta_{Mt})}{\log(2)}$$

Here the numerator equals the regional Shannon entropy excess that was actually observed in the region consisting of the two sampling units, and the denominator equals the regional Shannon entropy excess that would have been obtained if the two sampling units had shared no species. In other words, the Horn index of heterogeneity ranges Shannon entropy excess to the interval [0, 1], and therefore expresses the observed Shannon entropy excess as a proportion of its theoretical maximum value (given the observed mean species diversity in the sampling units and the number of sampling units observed). Although Horn (1966) derived the index for $N = 2$, it can easily be applied to datasets with $N \geq 2$. The generalisations of both Horn indices to N sampling units are simply

$$R_{hN} = \frac{\log({}^{1}\beta_{Mt})}{\log(N)} = 1 - R_{oN}$$

The C_{qN} measure of Chao et al. (2008) yields R_{oN} in the limit as q approaches unity (Jost 2006), but as we saw in Sections 4 and 5, C_{qN} corresponds to other definitions of "beta diversity" with other values of q.

It is obvious from the above equation that R_{hN} does not equal ${}^{1}\beta_{Mt}$ even though it is derivable from ${}^{1}\beta_{Mt}$. As mentioned in Section 1 (*Heterogeneity measures*), MacArthur (1965) used $\exp(H'_{\text{obs}} - H'_{\min}) = {}^{1}\beta_{Mt}$ as a measure of the faunal difference between two censuses. The

relationship with MacArthur's index was pointed out by Horn (1966) when discussing the new R_h measure.

7. Regional variance excess ${}^2\bar{\lambda}_{\gamma j-\gamma} = {}^2\bar{\lambda}_{\gamma j} - {}^2\lambda_{\gamma}$

Let us now apply the additive diversity index partitioning to the Gini-Simpson index $1-{}^2\lambda$:

$$\beta' = \gamma' - \alpha' = (1-{}^2\lambda_{\gamma}) - (1-{}^2\bar{\lambda}_{\gamma j}) = {}^2\bar{\lambda}_{\gamma j} - {}^2\lambda_{\gamma}$$

where $1-{}^2\bar{\lambda}_{\gamma j}$ equals the weighted arithmetic mean of the Gini-Simpson index values quantified for each sampling unit separately. Replacing β' with the more explicit annotation ${}^2\bar{\lambda}_{\gamma j-\gamma}$ and inserting ${}^2\lambda = 1/{}^2D$, the above equation can be re-expressed

$${}^2\bar{\lambda}_{\gamma j-\gamma} = 1 / {}^2\bar{D}_{\gamma j} - 1 / {}^2D_{\gamma} = ({}^2D_{\gamma} - {}^2\bar{D}_{\gamma j})/({}^2D_{\gamma}\,{}^2\bar{D}_{\gamma j})$$

where ${}^2\bar{D}_{\gamma j}$ is the weighted harmonic mean of the ${}^2D_{\gamma j}$ values. The equation can also be written

$${}^2\bar{\lambda}_{\gamma j-\gamma} = 1/\alpha_t - 1/\gamma = (\gamma - \alpha_t)/(\gamma\alpha_t)$$

When an individual is repeatedly picked at random from the sample, the Gini-Simpson index equals the variance in observed species identity, i.e. $\Sigma_{i=1}^{S}[p_i(1-p_i)]$ (Lande 1996, Couteron and Pélissier 2004). ${}^2\bar{\lambda}_{\gamma-\gamma j}$ can be called *regional variance excess* because it quantifies *the amount by which the variance in species identity of a randomly picked individual as calculated in the regional dataset exceeds that within a single sampling unit of arithmetic mean variance*.

From the formulation $1-\Sigma_{i=1}^{S}p_i^2$ it can be seen that the Gini-Simpson index also quantifies the probability that two individuals drawn at random (with replacement) from a sample are different species. Therefore, regional variance excess can also be interpreted as *the difference in the probabilities of drawing two individuals of different species in the entire dataset vs within a sampling unit of mean probability*. The generalisation of the Gini-Simpson index to other values of $q>1$ is $1-{}^q\lambda$, which quantifies the probability that q individuals drawn at random (with replacement) from a sample represent at least two different species. Consequently, inserting $1-{}^q\lambda$ into the equation $\beta' = \gamma' - \alpha'$ would yield a different definition of the beta component for each different value of q. To my knowledge, values of q other than 2 have not been used in connection with "additive beta diversity".

Regional variance excess is related to regional diversity excess by ${}^2\bar{\lambda}_{\gamma j-\gamma} = {}^2\beta_{At}/\gamma\alpha_t$, to Whittaker's effective species turnover by ${}^2\bar{\lambda}_{\gamma j-\gamma} = {}^2\beta_{Mt-1}/\gamma$ and to proportional effective species turnover by ${}^2\bar{\lambda}_{\gamma j-\gamma} = {}^2\beta_{Pt}/\alpha_t$. These equations show that regional variance excess quantifies *the amount of relative effective species turnover per effective species in the dataset*. Consequently, the amount of regional variance excess is mostly determined by the species diversity of the system: when α_t and γ increase, ${}^2\bar{\lambda}_{\gamma j-\gamma}$ necessarily approaches zero (see also Jost 2006, 2007). If all sampling units have equal weights, regional variance excess is constrained by an upper limit of $(N-1)/N\alpha_t$, which is obtained when none of the N sampling units share any species. Its absolute minimum value of zero is obtained when there is no variation in species proportional abundances among sampling units.

The dependence of regional variance excess on species diversity can be verified by the thought experiment of duplicating each species in the system: α and γ will double, but ${}^2\bar{\lambda}_{\gamma j-\gamma}$ will decrease by one-half. This is in contrast to the situation with absolute effective species turnover, which increases with increasing alpha diversity, and to that with the multiplicative beta components and the relative species turnover measures, which vary independently of alpha diversity. Consequently, if one wishes to rank regional datasets on the basis of their "beta diversity", regional variance excess will generally give results that are in conflict with results based on any of the other definitions. Interpreting trends in regional variance excess in terms of species turnover or compositional differences among sampling units can therefore be very misleading.

When quantified for two equally-weighted sampling units, regional variance excess equals the squared Euclidean distance between them as calculated using proportional abundance data (ter Braak 1983). The D_{ST} index, which is commonly used in genetical studies (Nei 1973, Jost 2008), is mathematically the same as regional variance excess, although D_{ST} uses a γ-classification based on alleles rather than species.

Just like regional diversity excess ${}^0\beta_{At}$ and regional entropy excess $\bar{H}'_{\gamma-\gamma j}$, regional variance excess ${}^2\bar{\lambda}_{\gamma j-\gamma}$ has been used as a measure of "additive beta diversity" with the justification that measuring α', β' and γ' in the same units (in this case, $1/sp_E$) is an advantage (Lande 1996, Gimaret-Carpentier et al. 1998, Wagner et al. 2000, Fournier and Loreau 2001, Crist et al. 2003, Gering et al. 2003, Pélissier et al. 2003, Summerville et al. 2003, Couteron and Pélissier 2004, Davis 2005, Pélissier and Couteron 2007). The interpretational problems that follow have been discussed by Jost (2006, 2007).

∞. How (not) to generate more definitions of "beta diversity"

Exploring the basic definitions of "beta diversity" has revealed that new definitions can be created by at least four strategies: 1) by defining "diversity" in a new way, 2) by defining the alpha component in a new way, 3) by defining the relationship between gamma and alpha in a new way, and 4) by forgetting about alpha and gamma and defining beta by some other means. In strategy 1, numerous different measures can be used to quantify "diversity". For example:

A) true diversity ${}^qD$
B) Shannon entropy $H' = \log({}^1D)$
C) Gini-Simpson index $1-{}^2\lambda = 1-1/{}^2D$
D) Fisher's alpha
E)–Z) raw value of some other diversity index.

Obviously, it is important to make an explicit choice among the definitions of "diversity", because each of them quantifies a fundamentally different phenomenon. Option A provides the most suitable diversity measure for a general

standard for three main reasons. Firstly, ${}^qD$ is the only measure of those listed that has the doubling property: when the intuitive diversity of a system doubles, the value of ${}^qD$ also doubles (Hill 1973, Jost 2007). Secondly, the interpretation of ${}^qD$ is logical, for example ''effective number of species'' when quantifying species diversity and ''effective number of habitats'' when quantifying habitat diversity. Thirdly, the sensitivity of ${}^qD$ to rare vs abundant species (or any other types of interest) can be adjusted by varying the value of q, without changing the interpretation of the measure or its measurement unit. The options corresponding to different values of q can be annotated A_q. For example, in option A_0 no importance is given to species abundances whereas in option A_1 the diversity value is affected by each species in proportion to its proportional abundance, but what is being measured in both cases is the number of effective species. In contrast, each of the other ''diversity'' measures corresponds to a different concept of ''diversity'' and will be associated with a different measurement unit. In the case of option B, the variants corresponding to different logarithm bases b can be annotated B_b.

In strategy 2, at least three different definitions of the alpha component of total ''diversity'' have been used, which can be derived from:

A) diversity per compositional unit α_d, e.g. ${}^qD_\alpha$ or H'_α
B) mean diversity in the original sampling units α_t, e.g. ${}^q\bar{D}_{\gamma j}$ or $\bar{H}'_{\gamma j}$
C) diversity of species-sampling unit combinations divided by diversity of sampling units α_R, e.g. ${}^qD_{\gamma\omega'/\omega}$.

The difference between options A and B is in the ecological interpretation and measurement units, as their numerical values are the same. In contrast, option C leads to numerically different results except in some special cases when it converges on option B.

In strategy 3, at least four equations have been used to calculate the beta component:

A) $\beta = \gamma/\alpha$
B) $\beta = \gamma - \alpha$
C) $\beta = (\gamma - \alpha)/\alpha$
D) $\beta = (\gamma - \alpha)/\gamma$.

Each of these equations leads to measuring something different, and therefore to defining a conceptually different beta component. Option A provides the most suitable equation for a general standard because it is the simplest way of producing independent alpha and beta components. Specific choices made with respect to strategies 1 and 2 limit the choices available for strategy 3. Let's say that option A was chosen in strategy 1. If we then choose option B in strategy 2, the measurement unit in both gamma and alpha diversity is sp_E and hence any of the strategy 3 options can be chosen. However, if we instead choose option A in strategy 2, then alpha diversity is measured using the unit sp_E/CU, which is not commensurate with sp_E. Thereby α cannot be subtracted from γ, which forces us to choose option A in strategy 3. The resulting beta component corresponds to true beta diversity ${}^q\beta_{Md}$, which can also be expressed as beta diversity based on strategy $1A_q$, 2A, 3A, or strategy $\beta(A_qAA)$, for short (Fig. 1).

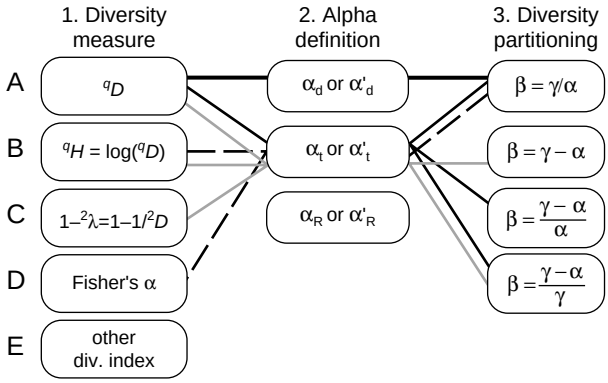

Figure 1. The beta component of ''diversity'' is defined by choosing 1) a diversity measure, 2) a definition for the alpha component and 3) a relationship between the alpha and gamma components. When option A is chosen in each case, true alpha, beta and gamma diversities are obtained; these choices are connected with thick black lines. The choices made by Whittaker (1960, 1972) when discussing ''beta diversity'' are connected with thin black lines; of these, the ones with stippled lines were rejected by Whittaker (1972). The choices connected by gray lines correspond to definitions of ''beta diversity'' proposed by Lande (1996). For explanation of the symbols, see Table 2.

The fourth strategy boils down to inventing a new dissimilarity index and calling whatever it quantifies ''beta diversity''. This strategy has been quite popular ever since Whittaker (1960, 1972) used the Jaccard and Sørensen indices and the percentage similarity to quantify ''beta diversity''. The review of Koleff et al. (2003a) listed 24 different indices that have been used to quantify ''beta diversity'' for presence-absence data, and Ricotta and Burrascano (2009) suggested that any meaningful dissimilarity index can be used for the purpose. The problem with this approach is that it leads to a proliferation of conceptually different definitions of ''beta diversity''. The dissimilarity indices that were mentioned in Sections 1 through 7, above, can be derived from alpha and gamma diversity. Therefore, each of them is compatible with one definition of ''beta diversity'', but a different definition in each case. Many other popular dissimilarity indices cannot be expressed as a function of γ and α at all. This seems to be the case with the chi-square metric, chord distance and Hellinger distance. The use of these indices may still be justified when addressing ecological questions related to compositional differences, but the results cannot be interpreted in terms of the alpha, beta and gamma components of diversity.

The conceptual interpretation of some dissimilarity measures changes depending on which kind of abundance data are used. This is especially obvious in the case of the squared Euclidean distance: using presence-absence data leads to quantifying regional diversity excess ${}^0\beta_{At}$, using proportional abundance data leads to quantifying regional variance excess ${}^2\bar{\lambda}_{\gamma-\gamma j}$ and using absolute abundance data leads to a dissimilarity measure that cannot be expressed as a function of α and γ. A number of indices converge on the Sørensen index (or its one-complement) when applied to

presence-absence data, and then quantify Whittaker's species turnover ${}^{0}\beta_{Mt-1}$. This is true of the percentage similarity used by Whittaker (1960) in his example 2, and the measures known as the Renkonen, Steinhaus, Odum and Bray-Curtis indices. However, there is no obvious way to express these indices in terms of α and γ when proportional or absolute abundance data are used.

A few examples of studies that have (unintentionally) used strategies 1 through 4 to create new definitions of "beta diversity" may be mentioned. Whittaker (1960, 1972) himself used most of them. One of the "beta diversity" measures that he proposed is regional-to-local diversity ratio β_{Mt}, which corresponds to strategy β(ABA) (Fig. 1). Whittaker used β_{Mt} with both $q=0$ and $q=1$, which can be expressed $\beta(A_0BA)$ and $\beta(A_1BA)$, respectively. Whittaker's species turnover β_{Mt-1} makes the same choices in strategies 1 and 2 but partitions gamma using a different equation, and corresponds to strategy $\beta(A_0BC)$ when applied to presence-absence data. Whittaker's use of the Jaccard index corresponds to using the ranged version of $\beta(A_0BD)$. Whittaker's discarded definitions were based on a ratio of Fisher's alphas or Shannon entropies, and correspond to strategies β(DBA) and $\beta(B_eBA)$, respectively. Whittaker's use of percentage similarity applied strategy 4, as this measure is not a function of α and γ. Whittaker's use of the half-change unit introduced a completely new approach, namely quantifying the amount of change in the chosen kind of beta component in relation to an external gradient; this and other derived approaches will be considered in the second part of the present review (Tuomisto 2010).

Although Hill (1973) made it obvious that he preferred numbers equivalents of diversity indices as the measure of diversity, he tentatively conceded that Rényi entropies might be used as well. The Rényi entropy of order q equals (Rényi 1960, Hill 1973)

$$ {}^{q}H = \frac{1}{1-q}\log\sum_{i=1}^{S} p_i^q = \log\sum_{i=1}^{S}(p_i^q)^{1/(1-q)} = \log({}^{q}D) $$

and is therefore a generalisation of the Shannon entropy $\log({}^{1}D)$ to values of q other than unity. Measuring "diversity" with the Rényi entropy therefore logically leads to a whole family of "beta diversity" concepts, namely $\beta(B_{q,b}++)$ where the expanded option B of strategy 1 (with subscripts to specify the value of q and the log base b) is combined with each of the options in strategies 2 and 3 in turn. It is clearly not desirable to call all these measures "beta diversity", because none of them quantifies the same phenomenon as does true beta diversity, strategy $\beta(A_qAA)$.

When Lande (1996) proposed defining "beta diversity" on the basis of additive partitioning of concave diversity indices ($\beta'=\gamma'-\alpha'$) instead of multiplicative partitioning of true diversities ($\beta=\gamma/\alpha$), in effect he introduced a host of new definitions of "beta diversity". He discussed three of these in detail, namely the ones based on species richness, Shannon entropy and the Gini-Simpson index. These correspond to strategies $\beta(A_0BB) = {}^{0}\beta_{At}$ (Section 3, above), $\beta(B_{1,e}BB) = \bar{H}'_{\gamma-\gamma j}$ (Section 6) and $\beta(CBB) = {}^{2}\bar{\lambda}_{\gamma-\gamma j}$ (Section 7), respectively. Many studies have applied two or three of these measures in parallel with the intention of studying how the alpha and beta components of diversity are affected when different relative weights are given to common vs rare species (DeVries et al. 1997, Wagner et al. 2000, DeVries and Walla 2001, Crist et al. 2003, Gering et al. 2003, Summerville et al. 2003, Ribeiro et al. 2008), or have discussed related analytical methods (Lande 1996, Pélissier et al. 2003, Couteron and Pélissier 2004, Couteron and Ollier 2005, Pélissier and Couteron 2007). However, when raw diversity index values are used, each diversity index not only weights species differently but also defines diversity itself in a different way. This causes a new definition of "beta diversity" to be created for each new diversity index, namely strategy $\beta(+BB)$. I have found only one study (Chandy et al. 2006) that conducted additive diversity partitioning for several values of q in parallel such that ${}^{q}D$ was used as the diversity measure. This is necessary for the results obtained with different diversity indices to quantify the same phenomenon (${}^{q}\beta_{At}$ in the case of Chandy et al. 2006) and hence to shed light on the effect of rare vs abundant species on that phenomenon. In genetic studies (where the γ-classification is based on alleles rather than species), β(CBB) is known as the D_{ST} index (Nei 1973, Jost 2008).

Lande (1996) further proposed using $\alpha'/\gamma' = (\gamma'-\beta')/\gamma' = 1-\beta'/\gamma'$ as a measure of community similarity, and observed that when species richness is used as the diversity index, this equals the inverse of Whittaker's beta diversity ($1/{}^{0}\beta_{Mt}$ in the current annotation). The corresponding dissimilarity index is $\beta'/\gamma' = (\gamma'-\alpha')/\gamma' = 1-\alpha'/\gamma'$. When based on species richness, this measure equals $({}^{0}D_{\gamma} - {}^{0}\bar{D}_{\gamma j})/{}^{0}D_{\gamma} = {}^{0}\beta_{Pt}$, which was discussed as a variant of "beta diversity" in Section 5 (above), and can now be classified as strategy $\beta(A_0BD)$. With Shannon entropy, β'/γ' becomes $(H'_{\gamma} - \bar{H}'_{\gamma j})/H'_{\gamma} = \bar{H}'_{\gamma-\gamma j}/H'_{\gamma}$ for which the strategic annotation is $\beta(B_{1,e}BD)$. This measure was used in a classic study on human genetic diversity by Lewontin (1972). With the Gini-Simpson index, β'/γ' becomes $[(1-{}^{2}\lambda_{\gamma}) - (1-{}^{2}\bar{\lambda}_{\gamma j})]/(1-{}^{2}\lambda_{\gamma}) = {}^{2}\bar{\lambda}_{\gamma j-\gamma}/(1-{}^{2}\lambda_{\gamma})$ whose strategic annotation is β(CBD). In genetic studies, β(CBD) is known as the G_{ST} index (Nei 1973, Jost 2008).

If β'/γ' is equated with "beta diversity", then a new variant of "beta diversity" is generated for each new diversity index used, namely strategy $\beta(+BD)$. Several researchers have used these measures to quantify compositional (dis)similarity between sampling units (DeVries et al. 1997, DeVries and Walla 2001, Fournier and Loreau 2001, Ricotta 2003, Munos et al. 2008). However, the interval over which the values of $(\gamma'-\alpha')/\gamma'$ vary depends on which measure is used, which complicates interpretation. In the case of $\beta(B_{1,e}BD)$, the possible range of values is $[0, \ln(N)/\ln(N\alpha_t)]$. In the other cases, $q \neq 1$ so a maximum value can be defined only when all sampling unit weights are equal. If this is the case, the range of values is $[0, (N-1)/N]$ for $\beta(A_0BD)$ and $[0, (N-1)/(N\alpha_t-1)]$ for β(CBD). Note the presence of α_t in two of the range definitions; it indicates that the value of $(\gamma'-\alpha')/\gamma'$ is independent of alpha diversity only when the diversity index in question has the doubling property. This easily causes interpretational problems when α varies among datasets (Jost 2006, 2007, 2008). Note also that all maximum values are dependent on N, which easily causes interpretational problems when N varies among datasets.

Each one of the β(+BB) and β(+BD) measures proposed by Lande (1996) quantifies some real property of the data, but a different property in each case. Neither family of measures quantifies either true beta diversity of a dataset or compositional differentiation among sampling units, so interpreting them as if they did leads to erroneous conclusions.

The C_{qN} measure of Chao et al. (2008), referred to in Sections 4, 5 and 6 (above), provides a compositional overlap index that is independent of the species richness of the system at all values of q (if $q \neq 1$, all sampling unit weights have to be equal). C_{qN} is calculated as follows:

$$C_{qN} = \frac{(\alpha_t/\gamma)^{q-1} - (1/N)^{q-1}}{1 - (1/N)^{q-1}} = \frac{(1/{}^{q}\beta_{Mt})^{q-1} - (1/N)^{q-1}}{1 - (1/N)^{q-1}}$$

At $q = 2$, this gives the same result as the equation of ${}^{q}C_{JN}$ (Section 5). The exponent is positive at $q > 1$, but becomes negative at $q < 1$ and therefore causes all terms to be inverted. The equation can then be restated with non-negative exponents as

$$C_{qN} = \frac{{}^{q}\beta_{Mt}{}^{1-q} - N^{1-q}}{1 - N^{1-q}} = \frac{N^{1-q} - {}^{q}\beta_{Mt}{}^{1-q}}{N^{1-q} - 1}$$

At $q = 0$, this gives the same result as the equation of ${}^{q}C_{SN}$ (Section 4), and in this case C_{qN} is linearly related with ${}^{q}\beta_{Mt}$. As q increases, the exponent causes the relationship between C_{qN} and ${}^{q}\beta_{Mt}$ to become increasingly curvilinear.

As an index of compositional overlap, C_{qN} has attractive properties (Jost 2006, Chao et al. 2008; see also Sections 4, 5 and 6). The general tendency in the ecological literature to interpret one-complements of similarity indices as "beta diversity" calls for a few words of caution, however. C_{qN} is based on ${}^{q}\beta_{Mt}{}^{1-q}$ rather than on ${}^{q}\beta_{Mt}$ itself, so its interpretation in terms of beta diversity is different for each value of q. When $q = 0$, C_{0N} is a linear transformation (given N) of regional-to-local diversity ratio ${}^{0}\beta_{Mt}$ and Whittaker's species turnover ${}^{0}\beta_{Mt-1}$ (Section 4). Its one-complement then equals the ranged version of strategies β(A_0BA) and β(A_0BC), respectively. In turn, C_{2N} is a linear transformation (given N) of proportional species turnover ${}^{2}\beta_{Pt}$ (Section 5), and $1 - C_{2N}$ equals the ranged version of strategy $1/\beta(A_2BA)$. In the limit, as q approaches unity, C_{1N} is a linear transformation (given N) of regional Shannon entropy excess $\bar{H}'_{\gamma-\gamma j}$ (Section 6), and $1 - C_{1N}$ equals the ranged version of strategies β($B_{1,b}$BA) and log[β(A_1BA)]. In general, C_{qN} is linearly related with strategy $1/[\beta(A_qBA)]^{q-1} = [\beta(A_qBA)]^{1-q}$. This is linearly related with regional-to-local diversity ratio β(A_qBA) and true beta diversity β(A_qAA) only at $q = 0$. If C_{qN} were mistakenly (contrary to its intended use) assumed to represent either "beta diversity" or a linear transformation of "beta diversity" with all q, a different definition of "beta diversity" would be created for each different value of q.

Several recent papers have suggested taking phylogenetic relatedness into account when quantifying "beta diversity". Some of the proposed measures are not related to alpha and gamma diversity in any way (Izsak and Price 2001, Lozupone et al. 2007) and therefore create new definitions of "beta diversity" by strategy 4. Others use as a starting point the decomposition of total diversity (or the decomposition of a diversity index), and then modify the calculations by applying weights to species pairs according to the phylogenetic distance between them (Hardy and Senterre 2007). Graham and Fine (2008) promoted the use of measures that incorporate phylogenetic information to study the link between ecological and evolutionary processes, and suggested using the terms "phylogenetic beta diversity" and "phylobetadiversity" for them. Such measures may indeed be useful, but great care is needed to avoid muddling these new concepts as badly as has happened with the traditional measures of "beta diversity". It seems that a transparent and straightforward way of examining the contribution of higher taxonomical levels to beta diversity (or to the other multiplicative diversity components) could be achieved simply by using a hierarchical γ-classification, as discussed in Section 1 (*Hierarchical diversity partitioning*).

Conclusions

Any diversity component (α, β or γ) can be computed for any group of organisms. To allow accurate communication about what the components are, a few crucial definitions need to be stated at the outset. First, quantifying gamma diversity necessitates specifying the γ-classification: which of the entities of interest belong to which of the types of interest. Most ecological applications have been interested in species diversity, in which case the γ-classification is the classification of observed individuals (or other units of abundance) into species. However, the concept of diversity is general and the same mathematical arguments can be applied to any dataset in which entities are classified into types. For example, individuals could be classified into taxa of some other rank than species (such as genera or families), into types defined by the presence of different alleles of a gene, or into ecological guilds, functional groups or size classes (as long as any given individual can belong to only one type). Similarly, entries in a species list could be classified into types on the basis of, say, the number of letters they contain, or characters in a species list could be classified into types on the basis of which letter they represent. To avoid confusion, it seems safest to restrict the use of the terms *γ-classification* and *gamma diversity* to taxonomical classes such as species, and to use other terms to refer to diversity related to other kinds of classifications.

If gamma diversity is to be partitioned into alpha and beta components, a second classification of the entities of interest is needed. The ω-classification defines which entities were observed in which sampling units. Changing the ω-classification by splitting or pooling sampling units leads to different proportions of the total diversity being apportioned to the alpha vs. the beta component. Attention must also be paid to sampling unit weights when calculating alpha and gamma diversity: these define whether the diversity components are quantified for the original dataset or for a new dataset with modified abundance values.

Once the γ-classification and the ω-classification have been defined, it is possible to proceed to defining diversity and its components. First, one must specify which measure is being used to quantify ''diversity'', what the alpha component represents, and which equation is being used to relate alpha and gamma diversities to each other when quantifying the beta component. True beta diversity is the number of compositional units in the dataset. It is obtained as $\beta_{Md} = \gamma/\alpha_d$ where true gamma diversity is the total effective number of species in the dataset, and true alpha diversity is the effective number of species per compositional unit, with each compositional unit having the same effective number of species as the real sampling units do on average. These diversity components are ecologically meaningful and provide a unified foundation for discussions concerning patterns and processes in diversity.

Each of the other ways of partitioning true gamma diversity or a gamma diversity index value can also be useful in specific ecological applications. However, their beta components do not quantify true beta diversity but other phenomena, such as absolute or relative turnover of effective species, ratio of regional to local species diversity, or the amount by which total entropy or variance exceeds the average entropy or variance of a single sampling unit. Accurate communication about these phenomena requires that each is identified by its own unique name.

Acknowledgements – I thank Robert K. Colwell for inviting me to write this review, for support during the process and for many useful comments on several versions of the manuscript. Numerous discussions with Kalle Ruokolainen on beta diversity and related issues have inspired and helped structure the contents of this paper. Helpful suggestions were also given by Mark Higgins, Mirkka Jones, Juhani Karhumäki, Esa Lehikoinen and especially four anonymous reviewers. The Academy of Finland provided funding that enabled my almost total immersion in the theme of beta diversity.

References

Allan, J. D. 1975a. Components of diversity. – Oecologia 18: 359–367.

Allan, J. D. 1975b. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. – Ecology 56: 1040–1053.

Arita, H. et al. 2008. Species diversity and distribution in presence–absence matrices: mathematical relationships and biological implications. – Am. Nat. 172: 519–532.

Arita, H. T. and Rodríguez, P. 2002. Geographic range, turnover rate and the scaling of species diversity. – Ecography 25: 541–550.

Balvanera, P. et al. 2002. Patterns of β-diversity in a Mexican tropical dry forest. – J. Veg. Sci. 13: 145–158.

Barker, J. S. F. et al. 1983. Heterogeneity of the yeast flora in the breeding sites of cactophilic *Drosophila*. – Can. J. Microbiol. 29: 6–14.

Basset, Y. et al. 2008. Choice of metrics for studying arthropod responses to habitat disturbance: one example from Gabon. – Insect Conserv. Divers. 1: 55–66.

Belmaker, J. et al. 2008. Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. – Ecology 89: 2829–2840.

Blackburn, T. M. and Gaston, K. J. 1996. The distribution of bird species in the New World: patterns in species turnover. – Oikos 77: 146–152.

Bratton, S. P. 1975. A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. – Bull. Torrey Bot. Club 102: 55–60.

Chandy, S. et al. 2006. Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. – J. Appl. Ecol. 43: 792–801.

Chao, A. et al. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. – Biometrics 62: 361–371.

Chao, A. et al. 2008. A two-stage probabilistic approach to multiple-community similarity indices. Biometrics 64: 1178–1186.

Chiarucchi, A. et al. 2008. Quantifying plant species diversity in a Natura 2000 network: old ideas and new proposals. – Biol. Conserv. 141: 2608–2618.

Chust, G. et al. 2006. Determinants and spatial modeling of tree β-diversity in a tropical forest landscape in Panama. – J. Veg. Sci. 17: 83–92.

Clarke, A. and Lidgard, S. 2000. Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. – J. Anim. Ecol. 69: 799–814.

Cody, M. L. 1975. Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Univ. Press, pp. 214–257.

Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. – Phil. Trans. R. Soc. B 345: 101–118.

Condit, R. et al. 2002. Beta-diversity in tropical forest trees. – Science 295: 666–669.

Couteron, P. and Pélissier, R. 2004. Additive apportioning of species diversity: towards more sophisticated models and analyses. – Oikos 107: 215–221.

Couteron, P. and Ollier, S. 2005. A generalized, variogram-based framework for multi-scale ordination. – Ecology 86: 828–834.

Crist, T. O. and Veech, J. A. 2006. Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area. – Ecol. Lett. 9: 923–932.

Crist, T. O. et al. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. – Am. Nat. 162: 734–743.

Davis, A. L. V. et al. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. – J. Biogeogr. 26: 1039–1055.

Davis, E. B. 2005. Mammalian beta diversity in the Great Basin, western USA: palaeontological data suggest deep origin of modern macroecological structure. – Global Ecol. Biogeogr. 14: 479–490.

DeVries, P. J. and Walla, T. R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. – Biol. J. Linn. Soc. 74: 1–15.

DeVries, P. J. et al. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. – Biol. J. Linn. Soc. 62: 343–364.

Diserud, O. and Ødegaard, F. 2007. A multiple-site similarity measure. – Biol. Lett. 3: 20–22.

Economo, E. P. and Keitt, T. H. 2008. Species diversity in neutral metacommunities: a network approach. – Ecol. Lett. 11: 52–62.

Ellingsen, K. E. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. – Mar. Ecol. Prog. Ser. 218: 1–15.
Ellingsen, K. E. 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. – Mar. Ecol. Prog. Ser. 232: 15–27.
Ellingsen, K. E. and Gray, J. S. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? – J. Anim. Ecol. 71: 373–389.
Flores-Palacios, A. and García-Franco, J. G. 2008. Habitat isolation changes the beta diversity of the vascular epiphyte community in lower montane forest, Veracruz, Mexico. – Biodivers. Conserv. 17: 191–207.
Fournier, E. and Loreau, M. 2001. Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. – Landscape Ecol. 16: 17–32.
Freestone, A. L. and Inouye, B. D. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. – Ecology 87: 2425–2432.
Gallardo-Cruz, J. A. et al. 2009. β-Diversity and vegetation structure as influenced by slope aspect and altitude in a seasonally dry tropical landscape. – Landscape Ecol. 24: 473–482.
Gardezi, T. and Gonzalez, A. 2008. Scale dependence of species–energy relationships: evidence from fishes in thousands of lakes. – Am. Nat. 171: 800–815.
Gering, J. C. and Crist, T. O. 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. – Ecol. Lett. 5: 433–444.
Gering, J. C. et al. 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. – Conserv. Biol. 17: 488–499.
Gimaret-Carpentier, C. et al. 1998. Sampling strategies for the assessment of tree species diversity. – J. Veg. Sci. 9: 161–172.
Graham, C. H. and Fine, P. V. A. 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space and time. – Ecol. Lett. 11: 1265–1277.
Graham, C. H. et al. 2006. Habitat history improves prediction of biodiversity in rainforest fauna. – Proc. Nat. Acad. Sci. USA 103: 632–636.
Gray, J. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. – J. Exp. Mar. Biol. Ecol. 250: 23–49.
Gregorius, H.-R. and Gillet, E. M. 2008. Generalized Simpson-diversity. – Ecol. Model. 211: 90–96.
Hardy, O. J. and Senterre, B. 2007. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. – J. Ecol. 95: 493–506.
Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. – Ecology 78: 1898–1906.
Harrison, S. and Inoye, B. D. 2002. High β diversity in the flora of Californian serpentine 'islands'. – Biodivers. Conserv. 11: 1869–1876.
Harrison, S. et al. 1992. Beta diversity on geographic gradients in Britain. – J. Anim. Ecol. 61: 151–158.
Harrison, S. et al. 2006. Beta diversity and the scale-dependence of the productivity–diversity relationship: a test in the Californian serpentine flora. – J. Ecol. 94: 110–117.
Hernández, H. M. et al. 2008. Cactus species turnover and diversity along a latitudinal transect in the Chihuahuan Desert Region. – Biodivers. Conserv. 17: 703–720.
Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. – Ecology 54: 427–432.
Hof, C. et al. 2008. Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. – Global Ecol. Biogeogr. 17: 539–546.
Holland, R. F. and Jain, S. K. 1981. Insular biogeography of vernal pools in the central valley of California. – Am. Nat. 117: 24–37.
Horn, H. S. 1966. Measurement of ''overlap'' in comparative ecological studies. – Am. Nat. 100: 419–424.
Izsak, C. and Price, A. R. G. 2001. Measuring β-diversity using a taxonomic similarity index, and its relation to spatial scale. – Mar. Ecol. Prog. Ser. 215: 69–77.
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. 2008. G_{ST} and its relatives do not measure differentiation. – Mol. Ecol. 17: 4015–4026.
Jurasinski, G. et al. 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. – Oecologia 159: 15–26.
Keylock, C. J. 2005. Simpson diversity and the Shannon-Wiener index as special cases of a generalized entropy. – Oikos 109: 203–207.
Kiflawi, M. and Spencer, M. 2004. Confidence intervals and hypothesis testing for beta diversity. – Ecology 85: 2895–2900.
Klimek, S. et al. 2008. Additive partitioning of plant diversity with respect to grassland management regime, fertilisation and abiotic factors. – Basic Appl. Ecol. 9: 626–634.
Klop, E. and Prins, H. H. T. 2008. Diversity and species composition of West African ungulate assemblages: effects of fire, climate and soil. – Global Ecol. Biogeogr. 17: 778–787.
Koch, L. F. 1957. Index of biotal dispersity. – Ecology 38: 145–148.
Koleff, P. and Gaston, K. J. 2001. Latitudinal gradients in diversity: real patterns and random models. – Ecography 24: 341–351.
Koleff, P. et al. 2003a. Measuring beta diversity for presence–absence data. – J. Anim. Ecol. 72: 367–382.
Koleff, P. et al. 2003b. Are there latitudinal gradients in species turnover? – Global Ecol. Biogeogr. 12: 483–498.
Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. – Oikos 76: 5–13.
Lee, T. D. and La Roi, G. H. 1979. Bryphyte and understory vascular plant beta diversity in relation to moisture and elevation gradients. – Vegetatio 40: 29–38.
Legendre, P. and Legendre, L. 1998. Numerical ecology, 2nd English ed. – Elsevier.
Levins, R. 1968. Evolution in changing environments: some theoretical explorations. – Princeton Univ. Press.
Lewontin, R. C. 1972. The apportionment of human diversity. – Evol. Biol. 6: 381–398.
Linares-Palomino, R. and Kessler, M. 2009. The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. – J. Biogeogr. 36: 280–290.
Lira-Noriega, A. et al. 2007. Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. – Divers. Distrib. 13: 185–195.
Lozupone, C. A. et al. 2007. Quantitative and qualitative β diversity measures lead to different insights into factors that structure microbial communities. – Appl. Environ. Microbiol. 73: 1576–1585.
MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. – Am. Nat. 98: 387–397.
MacArthur, R. H. 1965. Patterns of species diversity. – Biol. Rev. 40: 510–533.
Magurran, A. E. 2004. Measuring biological diversity. – Blackwell.

McCune, B. and Antos, J. A. 1981. Diversity relationships of forest layers in the Swan Valley, Montana. – Bull. Torrey Bot. Club 108: 354–361.
Mena, J. L. and Vázquez-Domínguez, E. 2005. Species turnover on elevational gradients in small rodents. – Global Ecol. Biogeogr. 14: 539–547.
Munari, C. and Mistri, M. 2008. Biodiversity of soft-sediment benthic communities from Italian transitional waters. – J. Biogeogr. 35: 1622–1637.
Munos, F. et al. 2008. Beta diversity in spatially implicit neutral models: a new way to assess species migration. – Am. Nat. 172: 116–127.
Nei, M. 1973. Analysis of gene diversity in subdivided populations. – Proc. Nat. Acad. Sci. USA 70: 3321–3323.
Normand, S. et al. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. – Plant Ecol. 186: 161–176.
Novotny, V. and Weiblen, G. D. 2005. From communities to continents: beta diversity of herbivorous insects. – Ann. Zool. Fenn. 42: 463–475.
Novotny, V. et al. 2007. Low beta diversity of herbivorous insects in tropical forests. – Nature 448: 692–695.
Ødegaard, F. 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. – Biodivers. Conserv. 15: 83–105.
Pärtel, M. et al. 2001. Variation in species richness within and between calcareous (alvar) grassland stands: the role of core and satellite species. – Plant Ecol. 157: 203–211.
Passy, S. I. and Blanchet, F. G. 2007. Algal communities in human-impacted stream ecosystems suffer beta-diversity decline. – Divers. Distrib. 13: 670–679.
Patil, G. P. and Taillie, C. 1982. Diversity as a concept and its measurement. – J. Am. Stat. Assoc. 77: 548–561.
Peet, R. K. 1974. The measurement of species diversity. – Annu. Rev. Ecol. Syst. 5: 285–307.
Pélissier, R. and Couteron, P. 2007. An operational, additive framework for species diversity partitioning and beta-diversity analysis. – J. Ecol. 95: 294–300.
Pélissier, R. et al. 2003. Consistency between ordination techniques and diversity measurements: two strategies for species occurrence data. – Ecology 84: 242–251.
Perelman, S. B. et al. 2001. Cross-scale vegetation patterns of flooding Pampa grasslands. – J. Ecol. 89: 562–577.
Pielou, E. C. 1975. Ecological diversity. – Wiley.
Plotkin, J. B. and Muller-Landau, H. C. 2002. Sampling the species composition of a landscape. – Ecology 83: 3344–3356.
Porembski, S. et al. 1996. Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Taï, Ivory Coast). – J. Biogeogr. 23: 47–55.
Price, A. R. G. et al. 1999. Ocean-scale patterns of "biodiversity" of Atlantic asteroids determined from taxonomic distinctness and other measures. – Biol. J. Linn. Soc. 66: 187–203.
Rényi, A. 1960. On measures of entropy and information. – Proceedings of the 4th Berkeley Symposium on Mathematics, Statistics and Probability, pp. 547–561.
Rey Benayas, J. M. 1995. Patterns of diversity in the strata of boreal montane forest in British Columbia. – J. Veg. Sci. 6: 95–98.
Ribeiro, D. B. et al. 2008. Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. – Divers. Distrib. 14: 961–968.
Ricotta, C. 2003. Additive partition of parametric information and its associated β-diversity measure. – Acta Biotheor. 51: 91–100.
Ricotta, C. 2005. On hierarchical diversity decomposition. – J. Veg. Sci. 16: 223–226.
Ricotta, C. 2008. Computing additive β-diversity from presence and absence scores: a critique and alternative parameters. – Theor. Popul. Biol. 73: 244–249.
Ricotta, C. and Burrascano, S. 2009. Testing for differences in beta diversity with asymmetric dissimilarities. – Ecol. Indic. 9: 719–724.
Rodríguez, P. and Arita, H. T. 2004. Beta diversity and latitude in North American mammals: testing the hypothesis of covariation. – Ecography 27: 547–556.
Roschewitz, D. et al. 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. – J. Appl. Ecol. 42: 873–882.
Routledge, R. D. 1977. On Whittaker's components of diversity. – Ecology 58: 1120–1127.
Routledge, R. D. 1979. Diversity indices: which ones are admissible? – J. Theor. Biol. 76: 503–515.
Ruokolainen, K. et al. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? – J. Trop. Ecol. 23: 13–25.
Scheiner, S. M. and Rey-Benayas, J. 1994. Global patterns of plant diversity. – Evol. Ecol. 8: 331–347.
Schlacher, T. A. et al. 1998. Soft-sediment benthic community structure in a coral reef lagoon – the prominence of spatial heterogeneity and 'spot endemism'. – Mar. Ecol. Prog. Ser. 174: 159–174.
Shannon, C. E. 1948. A mathematical theory of communication. – Bell Syst. Tech. J. 27: 379–423.
Sobek, S. et al. 2009. Spatiotemporal changes of beetle communities across a tree diversity gradient. – Divers. Distrib. 15: 660–670.
Stoms, D. M. 1994. Scale dependence of species richness maps. – Professional Geogr. 46: 346–358.
Summerville, K. S. et al. 2003. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. – Conserv. Biol. 17: 1045–1057.
Sweeney, B. A. and Cook, J. E. 2001. A landscape-level assessment of understory diversity in upland forests of north-central Wisconsin, USA. – Landscape Ecol. 16: 55–69.
ter Braak, C. J. F. 1983. Principal components biplots and alpha and beta diversity. – Ecology 64: 454–462.
Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. – Ecography 33: 23–45.
Tuomisto, H. and Ruokolainen, K. 2005. Environmental heterogeneity and the diversity of pteridophytes and Melastomataceae in western Amazonia. – Biol. Skr. 55: 37–56.
Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. – Science 299: 241–244.
Tylianakis, J. M. et al. 2006. Spatial scale of observation affects α, β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. – J. Biogeogr. 33: 1295–1304.
Vazquez, J. A. and Givnish, T. J. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. – J. Ecol. 86: 999–1020.
Veech, J. A. and Crist, T. O. 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. – Global Ecol. Biogeogr. 16: 650–656.
Veech, J. A. et al. 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? – J. Veg. Sci. 12: 545–552.
Wagner, H. H. et al. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. – Landscape Ecol. 15: 219–227.

Weiher, E. and Boylen, C. W. 1994. Patterns and prediction of α and β diversity of aquatic plants in Adirondack (New York) lakes. – Can. J. Bot. 72: 1797–1804.
Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – Ecol. Monogr. 30: 279–338.
Whittaker, R. H. 1972. Evolution and measurement of species diversity. – Taxon 21: 213–251.
Whittaker, R. H. 1977. Evolution of species diversity in land communities. – Evol. Biol. 10: 1–67.
Whittaker, R. J. et al. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. – J. Biogeogr. 28: 453–470.
Wiersma, Y. F. and Urban, D. L. 2005. Beta diversity and nature reserve system design in the Yucon, Canada. – Conserv. Biol. 19: 1262–1272.
Wilson, M. V. and Shmida, A. 1984. Measuring beta diversity with presence–absence data. – J. Ecol. 72: 1055–1064.

Mathematical proofs

Proof 1. The Shannon entropy H' is calculated as

$$H' = -\sum_{i=1}^{S} p_i \log p_i = -\sum_{i=1}^{S} \log(p_i^{p_i})$$

This equals

$$H' = -\log(p_1^{p_1}) - \log(p_2^{p_2}) - \ldots - \log(p_S^{p_S})$$
$$= -\log(p_1^{p_1} p_2^{p_2} \ldots p_S^{p_S})$$

Since Σp_i equals unity by definition, $p_1^{p_1} p_2^{p_2} \ldots p_S^{p_S}$ is the weighted geometric mean of the p_i values and H' therefore equals

$$H' = -\log(\bar{p}_i) = \log\left(\frac{1}{\bar{p}_i}\right) = \log({}^1D)$$

Choosing the base of the logarithm corresponds to choosing the unit of measurement (Shannon 1948). With base 2 the unit is binary digit or bit, with base e natural digit or nat and with base 10 decimal digit or decit. The geometric mean itself is not affected by the unit of the entropy, so when H' is converted to its numbers equivalent $\exp(H') = \exp(\log({}^1D))$, the same true diversity is recovered no matter which log base is used, provided that the same base is used both in the exponential function and the logarithm.

Proof 2. To calculate mean species diversity within the sampling units α_t, the weighted generalised mean with exponent $q-1$ of the proportional abundances of all species within all sampling units is first obtained as

$$\bar{p}_{(i|j)\text{all}} = \sqrt[q-1]{\sum_{j=1}^{N} \sum_{i=1}^{S} p_{ij} p_{i|j}^{q-1}}$$

Because $p_{ij} = w_j p_{i|j}$ (Table 1), this can be rewritten

$$\bar{p}_{(i|j)\text{all}} = \sqrt[q-1]{\sum_{j=1}^{N} \sum_{i=1}^{S} w_j p_{i|j} p_{i|j}^{q-1}} = \sqrt[q-1]{\sum_{j=1}^{N} w_j \sum_{i=1}^{S} p_{i|j}^{q}}$$

On the other hand, species diversity within sampling unit j equals

$${}^qD_{\gamma j} = (\bar{p}_{(i|j)j})^{-1} = \left(\sqrt[q-1]{\sum_{i=1}^{S} p_{i|j} p_{i|j}^{q-1}}\right)^{-1}$$
$$= \left(\sum_{i=1}^{S} p_{i|j}^{q}\right)^{1/(1-q)}$$

from which follows that

$$\sum_{i=1}^{S} p_{i|j}^{q} = {}^q D_{\gamma j}^{\,1-q}$$

The overall mean of the within-sampling unit proportional abundances can therefore be written

$$\bar{p}_{(i|j)\text{all}} = \sqrt[q-1]{\sum_{j=1}^{N} w_j ({}^qD_{\gamma j})^{1-q}} = \left(\sum_{j=1}^{N} w_j ({}^qD_{\gamma j})^{1-q}\right)^{1/(q-1)}$$

The inverse of this gives mean species diversity within the sampling units

$${}^q\bar{D}_{\gamma j} = (\bar{p}_{(i|j)\text{all}})^{-1} = \left(\sum_{j=1}^{N} w_j ({}^qD_{\gamma j})^{1-q}\right)^{1/(1-q)}$$

This is the weighted generalised mean with exponent $1-q$ of the ${}^qD_{\gamma j}$ values.

Above, only the γ-classification is considered important, so the measurement unit of $p_{i|j}$ is (individuals/effective species)/individuals and the measurement unit of α_t becomes sp_E. If the β-classification is also considered important, the measurement unit of $p_{i|j}$ is (individuals/effective species)/(individuals/compositional unit), and the result corresponds to α_d with measurement unit sp_E/CU. Although the unit of abundance (here individual) is not explicit in the final measurement unit, different units of abundance lead to numerically different results.

Proof 3. The overall mean of the within-sampling unit proportional abundances can be written

$$\bar{p}_{(i|j)\text{all}} = \sqrt[q-1]{\sum_{j=1}^{N} w_j \sum_{i=1}^{S} p_{i|j}^{q}} = \sqrt[q-1]{\sum_{j=1}^{N} w_j {}^q\lambda_{\gamma j}}$$

Mean species diversity within the sampling units is the inverse of this generalised mean and equals

$${}^q\bar{D}_{\gamma j} = (\bar{p}_{(i|j)\text{all}})^{-1} = \sqrt[1-q]{\sum_{j=1}^{N} w_j {}^q\lambda_{\gamma j}} = \left(\sum_{j=1}^{N} w_j {}^q\lambda_{\gamma j}\right)^{1/(1-q)}$$

which is the numbers equivalent of the weighted arithmetic mean of the ${}^q\lambda_{\gamma j}$ values, with the row totals of Table 1 used as weights. At $q=1$, the mean species diversity within sampling units is obtained as the exponential of the weighted arithmetic mean of the corresponding Shannon entropies (Proof 1 and Routledge 1977, 1979)

$${}^1\bar{D}_{\gamma j} = \exp(\log(1/\bar{p}_{(i|j)\text{all}})) = \exp(\bar{H}'_{\gamma j}) = \exp\left(\sum_{j=1}^{N} w_j H'_{\gamma j}\right).$$

Proof 4. Jost (2007) calculated "alpha diversity" as

$$ {}^{q}D_{\gamma\omega'/\omega} = \left(\frac{\sum_{j=1}^{N} w_j^q ({}^{q}\lambda_{\gamma j})}{\sum_{j=1}^{N} w_j^q} \right)^{1/(1-q)} $$

The denominator can be rewritten

$$ {}^{q}D_{\omega} = \sqrt[1-q]{\sum_{j=1}^{N} w_j w_j^{q-1}} = \bar{w}_j^{-1} $$

which is the effective number of sampling units in the dataset (virtual rows, each with mean w_j in Table 1).

By inserting ${}^{q}\lambda_{\gamma j} = \sum_{i=1}^{S} p_{i|j}^q$, the numerator of ${}^{q}D_{\gamma\omega'/\gamma}$ can be rewritten

$$ {}^{q}D_{\gamma\omega'} = \sqrt[1-q]{\sum_{j=1}^{N} w_j^q \sum_{i=1}^{S} p_{i|j}^q} = \sqrt[1-q]{\sum_{j=1}^{N} \sum_{i=1}^{S} w_j^q p_{i|j}^q} $$
$$ = \sqrt[1-q]{\sum_{j=1}^{N} \sum_{i=1}^{S} (w_j p_{i|j})^q} $$

Because $p_{ij} = w_j p_{i|j}$ (Table 1), this equals

$$ {}^{q}D_{\gamma\omega'} = \sqrt[1-q]{\sum_{j=1}^{N} \sum_{i=1}^{S} p_{ij}^q} = \bar{p}_{ij}^{-1} $$

which is the effective number of species-sampling unit combinations in the dataset (virtual cells, each with mean p_{ij} in Table 1).