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IDEA AND PERSPECTIVE

Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area

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Abstract

Additive partitioning of species diversity is widely applicable to different kinds of sampling regimes at multiple spatial and temporal scales. In additive partitioning, the diversity within and among samples (α and β) is expressed in the same units of species richness, thus allowing direct comparison of α and β. Despite its broad applicability, there are few demonstrated linkages between additive partitioning and other approaches to analysing diversity. Here, we establish several connections between diversity partitions and patterns of habitat occupancy, rarefaction, and species–area relationships. We show that observed partitions of species richness are equivalent to sample-based rarefaction curves, and expected partitions from randomization tests are approximately equivalent to individual-based rarefaction. Additive partitions can also be applied to species–area relationships to determine the relative contributions of factors influencing the β-diversity among habitat fragments.

Keywords

Hierarchical design, local and regional diversity, nested sampling, null hypothesis, spatial scale, species richness, temporal scale.

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INTRODUCTION

Species diversity is distributed heterogeneously among habitats, landscapes and regions. Ecologists are increasingly interested in quantifying the heterogeneity in species diversity by comparing components of diversity that occur within (α) and among samples (β) at multiple sampling scales (Wagner *et al.* 2000; Crist *et al.* 2003; Gering *et al.* 2003; Ugland *et al.* 2003; Olszewski 2004; Martin *et al.* 2005; Roschewitz *et al.* 2005; Summerville & Crist 2005). Additive diversity partitions express α- and β-diversity in the same measurement units so that their relative importance can be easily quantified and interpreted. This property of diversity partitioning permits direct comparisons of α- and β-diversity components across spatial and temporal scales or land-use practices (Loreau 2000; Wagner *et al.* 2000; Fournier & Loreau 2001; Gering & Crist 2002; Crist *et al.* 2003; Gering *et al.* 2003; Martin *et al.* 2005; Roschewitz *et al.* 2005; Summerville & Crist 2005). Thus far, however, there are few established connections between additive partitions of diversity with well-established methods of analysing and interpreting species diversity. A notable exception is Olszewski's (2004) recognition of the linkage between additive partitions and rarefaction curves using Simpson's diversity.

The species–area relationship is an important tool for quantifying changes in species richness across a continuous range of spatial scales, from quadrats to continents (Shmida & Wilson 1985; Rosenzweig 1995; Lomolino 2000; Crawley & Harral 2001; Scheiner 2003; Drakare *et al.* 2006). Despite its generality, there are several limitations of the species–area relationship. First, for some organisms, samples from fixed areas are difficult to obtain, and species richness can only be expressed in units of sampling effort. Second, differences in the relative abundances of species are often ignored (Brewer & Williamson 1994; Gotelli & Colwell 2001). As demonstrated by Coleman *et al.* (1982), passive sampling of individuals may result in low species richness in small habitats simply because species with lower abundances are absent by chance. Third, as we demonstrate in this paper, β-diversity among habitats is only partly explained by habitat area. In many, if not most, species–area relationships, other

factors such as habitat heterogeneity, dispersal limitation and chance effects, may have a greater role in influencing patterns of β-diversity.

Species–accumulation curves are used to evaluate the effectiveness of sampling or to compare species richness among habitats using rarefaction (Colwell & Coddington 1994; Gotelli & Colwell 2001). Unlike species–area relationships, samples need not be area-based because rarefaction explicitly controls for differences in the numbers of individuals among samples (Brewer & Williamson 1994; Gotelli & Colwell 2001). Individual-based rarefaction provides the expected numbers of species with increasing numbers of individuals sampled, assuming a random sample of individuals in the community. Sample-based rarefaction describes the average number of accumulated species as the number of samples increases (Gotelli & Colwell 2001). The average number of species in sample-based rarefaction typically increases more slowly than in individual-based rarefaction because species are often aggregated in different sets of samples (Colwell *et al.* 2004). Recently, studies have examined species–accumulation curves from large sample areas or multiple years and compared them with those obtained from subsets of data to examine the role of spatial or temporal scale of sampling on species richness (Ugland *et al.* 2003; Summerville & Crist 2005). Such approaches provide an important step in quantifying the contributions of different habitats to broad-scale patterns of species richness or temporal patterns of richness within habitats.

Here, we provide a common framework for analysing species richness as a function of sampling effort, spatial scale, or habitat area using additive partitions of diversity. Our framework explicitly recognizes that α and β can be measured at different scales of sampling. Several other studies have examined how species richness varies with nested sampling areas of different sizes and its effects on nested species–area relationships (e.g. Shmida & Wilson 1985; Palmer & White 1994; Rosenzweig 1995; Leitner & Rosenzweig 1997; Crawley & Harral 2001; Arita & Rodríguez 2002; Cam *et al.* 2002; Drakare *et al.* 2006). In nested areas, species richness always grows with increasing sample area and larger areas contain all the species found in smaller areas. Here, we focus on spatially discrete samples – based on area, transects, or trapping effort – that may differ in their species composition. First, we consider the case where samples are arranged in a hierarchical or nested sampling design and relate additive diversity partitions to patch occupancy and rarefaction curves. Next, we apply additive partitioning to species–area relationships derived from isolated habitats. Finally, we compare results from additive and multiplicative partitions of diversity where appropriate.

ADDITIVE PARTITIONING OF DIVERSITY AT MULTIPLE SAMPLING SCALES

Ecologists routinely sample diversity using various sample units, such as quadrats, transects, or traps. Each sample unit has an alpha diversity and hence the mean alpha diversity (α_1) is obtained from a set of samples that represents the finest scale of sampling (i.e. the sample grain). A collection of sample quadrats, say from a given habitat, may be pooled together to form larger samples. Then, if several habitats are sampled, α_2 is the average diversity found within the set of habitats representing a second scale of sampling. Extending across multiple sampling scales, α_i is the average diversity found in a pooled set of samples for $i = 1, 2, 3 \ldots m$ levels of sampling. Thus, α_i may represent average diversity within quadrats, habitats, landscapes or even regions. In plot-based sampling, the size of the sample unit used to obtain α_1 is the sample grain, and the spatial extent for each $\alpha_{2\ldots m}$ depends on the spatial arrangement of samples. Let γ be the total species diversity found in the entire collection of samples, so that $\gamma \geq \alpha_m$ (Lande 1996). This operational definition of γ is the diversity in the total pooled set of samples, whether the set of samples is from a single habitat, landscape, or region. Let s_{ij} be the species richness recorded in each sample $j = 1,2,3 \ldots r_i$, where r_i is the number of samples at level i of the hierarchical sampling design. Modifying Lande's (1996) expression for multiple sampling levels, the average diversity (α_i) at each hierarchical level i is

$$\alpha_i = \frac{1}{r_i} \sum_{j=1}^{r_i} s_{ij}. \quad (1)$$

Samples are given equal weights in estimating α_i. The α_i components have also been estimated using samples that are weighted by the number of individuals in each sample (e.g. Wagner *et al.* 2000; Fournier & Loreau 2001; Crist *et al.* 2003). Here, we use equal weights, however, because only the α_i- and β_i-components of species richness calculated from equally weighted samples correspond to sample-based rarefaction curves (described later).

For additive partitions of nested sampling designs, the β-components are calculated as $\beta_m = \gamma - \alpha_m$ at the highest sampling level, and as $\beta_i = \alpha_{i+1} - \alpha_i$ for each lower sampling level (Wagner *et al.* 2000; Crist *et al.* 2003). Lande (1996) gave an expression to calculate β-diversity directly, which modified for hierarchical designs is:

$$\beta_i = \frac{1}{r_i} \sum_{j=1}^{r_i} (\gamma - s_{ij}). \quad (2)$$

Thus, β_i is the average diversity that is absent from given sample j (Veech *et al.* 2002; Crist *et al.* 2003). Following Crist

et al. (2003), the additive partition of diversity for multiple sampling levels is

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i. \quad (3)$$

Crist *et al.* (2003) presented a series of randomization tests for assessing the statistical significance of the α- and β-components from a partition. Program PARTITION (available at http://zoology.muohio.edu/partition) calculates observed partitions and conducts tests of significance using the randomization routines described in Crist *et al.* (2003). Individual-based randomization randomly allocates n_{ij} individuals to each sample j at the lowest hierarchical level $i = 1$. For partitioning of species richness, this is equivalent to the random placement model of Coleman *et al.* (1982) except that sample abundances are used rather than habitat areas. It is also approximately equivalent to individual-based rarefaction (Brewer & Williamson 1994) except that in individual-based randomization the expected species richness is based on the abundances of each sample n_{ij} rather than cumulative sample abundances.

We use butterfly assemblages to illustrate and compare additive partitioning of diversity to other methods. Butterflies were recorded in 26 small, isolated grassland remnants surrounded by a forest matrix at the Edge-of-Appalachia Preserve, Ohio, USA. Remnant habitat patches were small (0.1–2.5 ha) and scattered over a 25 km^2 area, but they were clumped into six clusters of three to nine patches on soils derived from calcareous rock outcrops. Patches within clusters were separated by an average of 0.26 km, whereas patches among clusters were separated by an average of 2.93 km. Patches and clusters of patches therefore formed a natural sampling hierarchy. Butterfly counts of each species were recorded along Pollard transects in five surveys of each patch conducted during summer 2004.

A total of $\gamma = 49$ species and 1334 individuals were recorded in the 26 patches. The Chao 2 estimate of species richness (Colwell & Coddington 1994) was 51 (using patches as sample units), so virtually all of the species present were likely sampled in this survey. Additive partitions of species richness showed that $\alpha_{patch} = 16.7$, $\beta_{patch} = 15.0$ ($\alpha_{cluster} = \alpha_{patch} + \beta_{patch} = 31.7$), and $\beta_{cluster} = 17.3$. An individual-based randomization test in program PARTITION showed that α_{patch} was lower than expected from random placement of individuals, β_{patch} was not significantly different from expected, and $\beta_{cluster}$ was significantly greater than expected. These results are consistent with the known dispersal abilities of butterflies in this system; mark-recapture of butterflies showed frequent dispersal among patches within clusters but not among clusters (T.O. Crist, unpublished data). Dispersal limitation and differences in habitat quality appear to contribute to the high levels of $\beta_{cluster}$ (T.O. Crist, unpublished data).

ADDITIVE PARTITIONING AND PATCH OCCUPANCY AT MULTIPLE SCALES

The partitioning of total species richness into α- and β-components is related to patch occupancy and range sizes of species. Whittaker's (1960) multiplicative partition $\gamma = \alpha\beta$ has been used to express β-diversity as the ratio of the maximum and the average range sizes of species (Schluter & Ricklefs 1993; Leitner & Rosenzweig 1997). More recently, Arita & Rodríguez (2002, 2004) used this approach to analyse how β-diversity varies with sampling scale when a region is sampled by a nested series of quadrats, and expressed β as the ratio of the total number of sites (or quadrats) sampled to the average site occupancy of all species. This approach can also be applied to additive definitions of β. First, we express γ as the product of α and β, with β defined as in Arita & Rodríguez (2002, 2004):

$$\gamma = \alpha_i \frac{r_i}{\bar{u}_i}, \quad (4)$$

where r_i is the total number of samples at level i, and $\bar{u}_i$ is the average number of samples (sites) occupied across all species γ. Thus, in multiplicative partitions, site occupancy is related to richness components as $\alpha_i = \frac{\bar{u}_i}{r_i}\gamma$ and $\beta_i = \frac{r_i}{\bar{u}_i}$ (Arita & Rodríguez 2002, 2004). Since α-diversity is the same for both multiplicative and additive partitions, we substitute the expression for α_i into the additive partition $\alpha_1 + \sum_{i=1}^{m} \beta_i = \gamma$, where m is the total number of sampling levels. Thus, the expressions for additive partitions for α-diversity at lowest level and the summed β-diversities at all levels are

$$\alpha_1 = \frac{\bar{u}_1}{r_1}\gamma \quad \text{and} \quad \sum_{i=1}^{m} \beta_i = \left(1 - \frac{\bar{u}_1}{r_1}\right)\gamma. \quad (5)$$

The total β-component ($\sum\beta_i$) can be decomposed into β_i components at sampling levels $i = 1 \ldots m$ by subtraction of the proportional α_i components as follows:

$$\beta_m = \left(1 - \frac{\bar{u}_m}{r_m}\right)\gamma \quad \text{and} \quad \beta_i = \left(\frac{\bar{u}_{i+1}}{r_{i+1}} - \frac{\bar{u}_i}{r_i}\right)\gamma, \quad (6)$$

where $\frac{\bar{u}_i}{r_i}$ is the α_i expressed as a proportion of γ for each sampling level i. Furthermore, if we define $\bar{p}_i = \frac{\bar{u}_i}{r_i}$ as the average incidence (the mean proportion of sites occupied) over all the species, then $\alpha_1 = \bar{p}_1\gamma$ and $\sum\beta_i = (1 - \bar{p}_1)\gamma$. These are equivalent to the expressions used by Kiflawi & Spencer (2004) to define additive components of species richness. Returning to the butterfly example with two sampling levels ($m = 2$), patches ($i = 1$) and clusters ($i = 2$),

the average number of patches occupied by the 49 butterfly species is $\bar{u}_1 = 8.86$ of $r_1 = 26$ total patches, or $\bar{p}_{\text{patch}} = 0.34$ and $\sum\beta_i = 0.66$. These values correspond to α_1 and $\sum\beta_i$ expressed as proportions of γ (16.7/49 = 0.34 and 32.3/49 = 0.66, respectively). At the next sampling scale, the average number of occupied clusters is $\bar{u}_2 = 3.88$ of $r_2 = 6$ clusters, or $\bar{p}_{\text{cluster}} = 0.65$. The total β, or $\sum\beta_i = 32.3$, can be decomposed into the proportional β_i-components for each sampling scale using eqn 6: $\beta_{\text{cluster}} = 1 - \bar{p}_{\text{cluster}} = 1 - 0.65 = 0.35$ and $\beta_{\text{patch}} = \bar{p}_{\text{cluster}} - \bar{p}_{\text{patch}} = 0.65 - 0.34 = 0.31$, which correspond to the proportional components $\beta_{\text{cluster}} = 17.3/49 = 0.35$ and $\beta_{\text{patch}} = 15/49 = 0.31$. Additive components of β-diversity can, therefore, be expressed as a function of site occupancy as it varies across sampling levels or spatial scales in a similar manner to previous studies that have examined these effects using multiplicative partitions (Schluter & Ricklefs 1993; Leitner & Rosenzweig 1997; Arita & Rodríguez 2002, 2004).

DIVERSITY PARTITIONING AND RAREFACTION CURVES

Rarefaction curves are plots of the cumulative species richness as a function of the numbers of individuals sampled. In individual-based rarefaction, the expected number of species is calculated by sampling from a hypergeometric distribution, which assumes that individuals of each species are randomly distributed among samples (Hurlbert 1971). The random placement model of Coleman *et al.* (1982) closely approximates individual-based rarefaction if the expected species richness is based on sample abundance rather than habitat area (Brewer & Williamson 1994). Sample-based rarefaction provides the expected numbers of species based on the average number of individuals per sample when samples are randomly drawn without replacement (Gotelli & Colwell 2001; Colwell *et al.* 2004). Hence, the latter preserves any species aggregation that is present in the samples. Until recently, sample-based rarefaction could only be conducted by simulation; however, companion studies by Colwell *et al.* (2004) and Mao *et al.* (2005) provide analytical solutions to sample-based rarefaction.

Rarefaction curves are often constructed from samples taken within habitats to determine the efficacy of sampling the true species richness of a given habitat, or to compare species richness among habitats on an equal-effort basis (Gotelli & Colwell 2001). Using a slightly different approach, Ugland *et al.* (2003) combined species–accumulation curves from samples of different habitats to produce subsets of the total species–accumulation curve. Their approach emphasizes that curves differ with habitat heterogeneity or spatial scales of sampling.

We build on these approaches by constructing a rarefaction curve for each sampling level in a hierarchically scaled design. This results in a series of curves in which higher levels contain smaller numbers of samples of larger size, all leading to the same total species richness. In the case of the butterfly data, there are two such curves, one for patches and one for clusters (Fig. 1a). This leads to the following relationships between sample-based rarefaction curves and diversity partitioning: (1) the total cumulative species richness corresponds to the γ-diversity, the number of species in the pooled set of samples; (2) the average species richness of the samples, the α_1-diversity, is the first point on the accumulation curve; (3) the difference in species richness between the last and first points is the total β-diversity among samples; and (4) the difference in species richness between

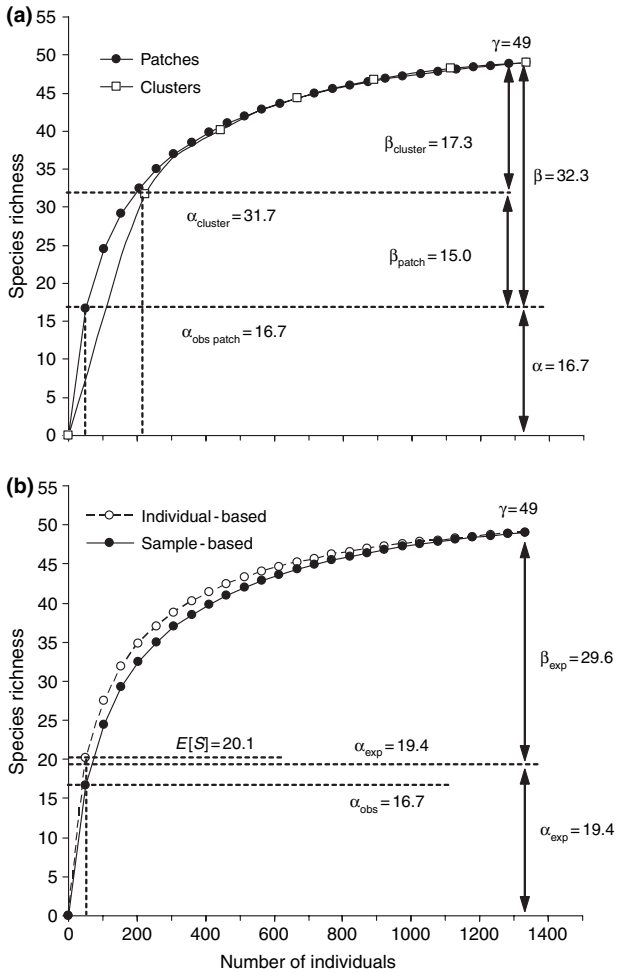

Figure 1 The relationship between the additive diversity partitions and rarefaction. (a) Observed components of species richness and sample-based rarefaction. (b) Expected components of species richness from individual-based randomization (α_{exp} and β_{exp}) and individual-based rarefaction (E[S]). The expected components for clusters are omitted.

the first sample points, the α_i for each sampling level, of each successive nested accumulation curve determines the size of each β_i component of species richness (Fig. 1a).

These parallels also suggest a relationship between the null hypothesis of individual-based randomization in PARTITION and individual-based rarefaction. In fact, for species richness the expected values from individual-based randomization can be calculated from Hurlbert's (1971) rarefaction formula (or approximated by Coleman's random placement model; Brewer & Williamson 1994); however, they differ in a subtle but important way. The expected value of α_{exp} from individual-based randomization in PARTITION is the average of the expected number of species found in each sample based on the number of individuals in each sample n_{ij} because individual-based randomization conserves sample size. The expected species richness from individual-based rarefaction is based on the number of species that are expected from the average sample size, $\widehat{n}_i = \frac{1}{r_i}\sum_{j=1}^{r_i} n_{ij}$. Because expected species richness as a function of sample size is nonlinear, expected values of species richness from individual-based randomization will be more affected by small samples than are those from rarefaction. Individual-based randomization therefore results in a lower α_{exp} (and more similar to the observed) than does rarefaction based on cumulative samples (Fig. 1b).

The relationship between observed partitions of α- and β-components of species richness and sample-based rarefaction merits further mention because analytical solutions were recently developed for sample-based rarefaction. These analytical expressions also provide the α- and β-components of species richness for additive partitions ($\alpha = \gamma - \beta$). Ugland *et al.* (2003) derived the following:

$$E[S(a)] = S_{obs} - \sum_{k=1}^{S_{obs}} q_k(a), \tag{7}$$

where $E[S(a)]$ is the expected species richness in the cumulative number of a samples (α_1 when $a = 1$), S_{obs} is the total number of species in all samples (γ), and $q_k(a)$ is the probability that a species k is not found in a set of a samples. The probability $q_k(a)$ depends on sample size n_j and numbers of samples a (Ugland *et al.* 2003). Thus, $\sum_{k=1}^{S_{obs}} q_k(a) = \beta$ when $a = 1$ because the difference between the species richness in the first and last samples in an accumulation curve is the total β-diversity. Similarly, Colwell *et al.* (2004) derived the following expression:

$$\tilde{\tau}(h) = S_{obs} - \sum_{l=1}^{H} c_{lh}\, x_l, \tag{8}$$

where x_l are the numbers of species found in exactly l samples ($l = 1$ sample, $l = 2$ samples, and so on), and c_{lh} are combinatorial coefficients that weight x_l depending on the occurrence of species as the number of samples h varies from 1 to H, the total number of samples. Here, as in eqn 5, $\tilde{\tau}(h) = \alpha_1$ and $\sum_{l=1}^{H} c_{lh}x_l = \beta$ when h = 1. As noted by Colwell *et al.* (2004), eqns 7 and 8 are equivalent expressions mathematically. Both of these analytical solutions for sample-based rarefaction are equivalent to hierarchical additive partitions of species richness, $\alpha_i = \gamma - \beta_i$, where α_i for $i = 1\ldots m$ occur as discrete hierarchical levels along the curve that correspond to the cumulative numbers of species $a = 1\ldots S_{obs}$ in eqn 7 or the species richness in the numbers of samples $h = 1\ldots H$ in eqn 8.

Rarefaction curves are often used to evaluate the adequacy of sampling by assessing whether the cumulative number of species has reached an asymptote, by comparing the S_{obs} to species-richness estimators, such as Chao2 or ICE, or by extrapolating the curve (Colwell & Coddington 1994; Ugland *et al.* 2003; Colwell *et al.* 2004). Using the relationship between sample-based rarefaction and additive partitions, we now ask how sampling effort affects observed values of α- and β-diversity by simulations that involve subsampling of the butterfly data (Fig. 2). If we had sampled only 13 of the 26 grassland patches, then the β- and γ-components of species richness would be underestimated compared with the whole data set because α remains constant while β and γ increase as the numbers of samples increases (Fig. 2). In contrast, the α-component is greater for those 13 samples containing the largest number of individuals compared with the 13 samples with the smallest number, so as the size of each sample increases, then α and γ increase (Fig. 2). Stated differently, the sample grain – the size of the sample unit or the number of individuals in the sample – affects the α-component of diversity, and the sample extent – the number and spatial arrangement of samples – affects the β-components of diversity. Together, both sample grain and extent affect γ-diversity. As it is defined here, γ is the value of interest when estimating the true species richness for a given area. Additive partitions of diversity do not provide estimates of the true γ, however, and are therefore not substitutes for rarefaction curves or species-richness estimators (Colwell 2004). Randomization tests to determine the statistical significance of differences in observed and expected diversity components are based on the observed numbers and sizes of the samples, and are therefore robust to sampling effort. Nonetheless, limited sampling effort reduces the statistical power to detect departures from null patterns (Crist *et al.* 2003; see also Kiflawi & Spencer 2004).

DIVERSITY PARTITIONING AND THE SPECIES–AREA RELATIONSHIP

Species–area relationships are variously constructed from isolated habitats or oceanic islands, or from nested sampling areas of increasing size (Rosenzweig 1995; Scheiner 2003). Here, we apply additive partitions to species–area relation-

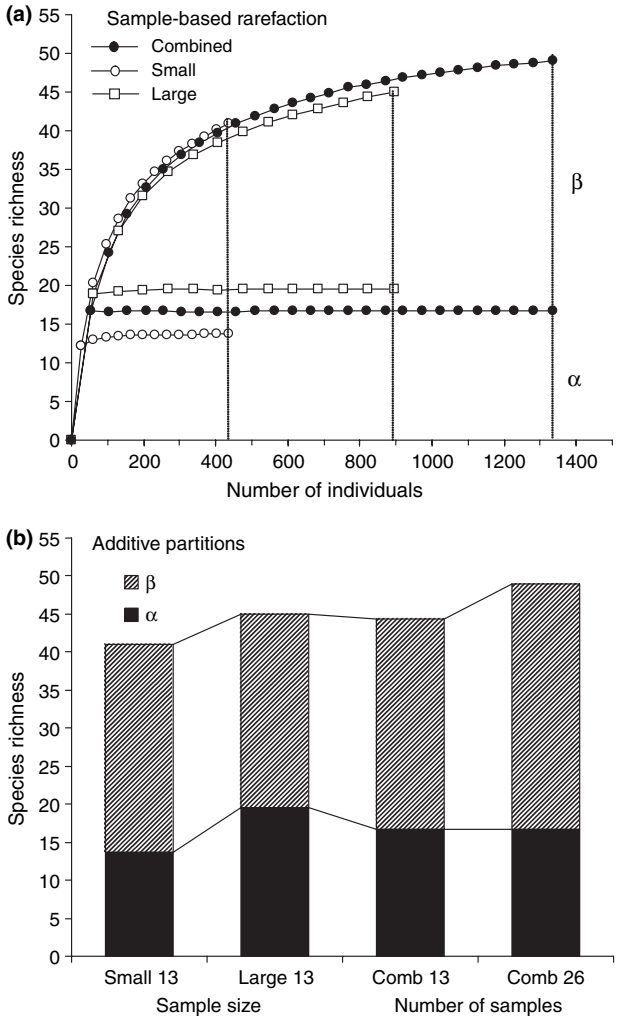

Figure 2 The effects of the numbers of samples and sample size on the observed components of species richness. (a) The 'combined' is all 26 samples, 'small' is the 13 samples containing the fewest number of individuals, and 'large' is the 13 samples containing the largest number of individuals. (b) The relative contributions of α- and β-components of species richness for all 26 combined samples, a random subset of 13 samples, the 13 smallest samples and the 13 largest samples.

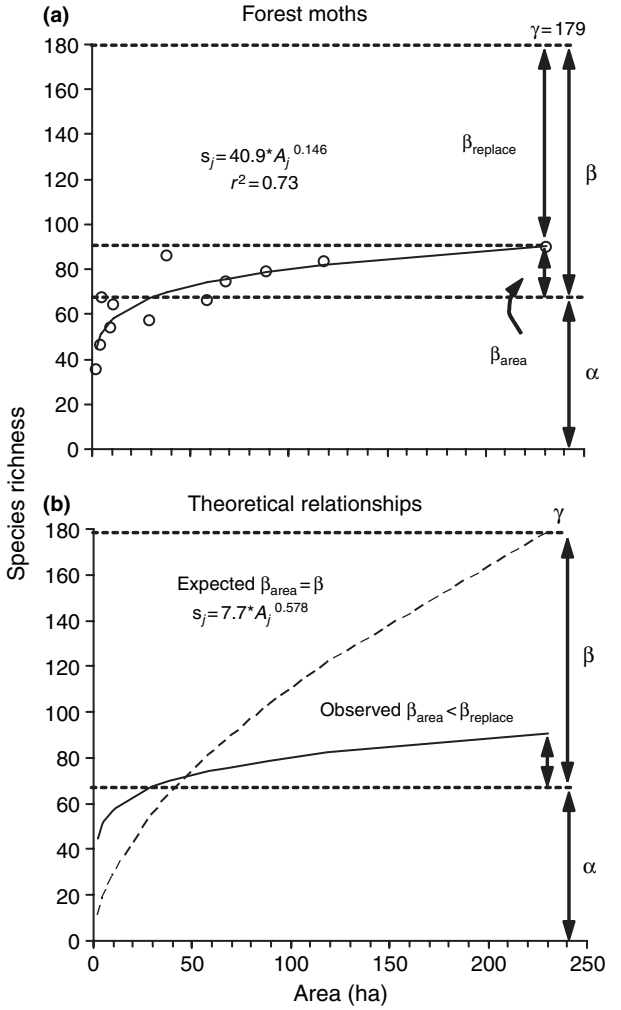

Figure 3 Additive partitioning of the species–area relationship. (a) The observed components of species richness for 179 moth species (γ) in forest fragments 2–230 ha in size. The regression between species richness and area has an $r^2 = 0.73$, but β_{area} explains only 0.13 of γ, while $\beta_{replace}$ comprises 0.49 of γ. (b) Comparison of the observed species–area relationship with the theoretical curve necessary for $\beta_{area} = \beta$, assuming the same α and γ as the observed.

ships derived from isolated habitats within a region or a group of oceanic islands. First, define the α-component of species richness as the average number of species observed in each habitat, calculated from all habitat patches, regardless of size. Of course, the area of a patch partly determines its species richness so the α-component is influenced by patch areas but the effect of area is averaged across all patches (Fig. 3a). As before, we define γ as the combined species richness found in all habitats. The β-component of species richness is determined by subtraction or by eqn 2. We now assess how much of the total β-diversity is due to area (β_{area}), and how much is due to other factors, which we call species replacement ($\beta_{replace}$). Let s_{max} equal the species richness of the largest habitat patch. We can estimate β_{area} by substituting s_{max} into eqn 2,

$$\beta_{area} = \frac{1}{r}\sum_{j=1}^{r}(s_{max} - s_j), \quad (9)$$

where s_j is the observed species richness in each habitat j, and r is the number of habitat patches. Thus, β_{area} is the mean deviation between the species richness of the largest habitat patch and the species richness of smaller patches.

In nested species–area relationships, all of the species present in small areas also occur in larger areas and the largest-area sample has s_{max}. In this special case, all of the β-diversity is due to area ($\beta_{area} = \beta$) because $s_{max} = \gamma$ and eqn 9 is identical to eqn 2. For non-nested areas, however, s_{max} is typically $\ll\gamma$ so that $\beta_{area} < \beta$. We define $\beta_{replace}$ as the β-diversity due to factors other than habitat area, such as among-patch heterogeneity, the surrounding matrix habitat, or chance effects. Thus, the additive partition for the species–area relationship is

$$\gamma = \alpha + \beta_{area} + \beta_{replace}. \quad (10)$$

In species–area relationships of isolated habitats, species richness often does not increase monotonically with habitat area because there is variability in s_j that is unrelated to area. Therefore, to ensure that s_{max} corresponds to the largest habitat area, we use the predicted values of s_{max} and s_j from a species–area regression in eqn 9 to estimate β_{area}. Least-squares regression retains additivity of α- and β-components because the predicted and observed values of α are equal. Here, we use the power-law species–area relationship ($s_j = kA_j^z$), but any least-squares regression model can be used without loss of generality.

We illustrate the calculation of β_{area} and $\beta_{replace}$ using a data set on forest-dwelling moths recorded in 12 forest fragments (size range 2–230 ha) in an agricultural landscape (Summerville & Crist 2004). This data set encompasses a range in habitat areas that is an order of magnitude larger than the butterfly data, but γ was not completely sampled as with the butterfly data. To eliminate matrix species, the 179 species that use woody plants for larval hosts were included in the analysis. The Chao 2 estimate of species richness was 209, so 86% of the estimated γ was sampled. Using a power-law regression, habitat area explained 73% of the variation in species richness among fragments (Fig. 3a). The additive partition of the species–area relationship showed that $\alpha = 66.7$ (37% of γ), $\beta_{area} = 23.8$ (13% of γ), and $\beta_{replace} = 88.5$ (49% of γ) (Fig. 3a). Thus, although species richness varies predictably with area, forest fragments have very different assemblages of moths (a large $\beta_{replace}$) due to factors other than area. If α and γ are held constant, one can find the slope and intercept of the species–area relationship that are necessary to produce $\beta_{area} = \beta$. For the moth data, an increase in the observed slope of $z = 0.146$–0.578, with a corresponding decrease in intercept, is necessary for $\beta_{area} = \beta$ (Fig. 3b).

The slope of the species–area relationship is often viewed as a measure of β-diversity among habitat areas, perhaps because of the parallel forms of the log-transformed form of the multiplicative partition $\log \gamma = \log \alpha + \log \beta$ and the log-transformed form of the power-law species–area relationship, $\log s_j = \log k + z \log A_j$. Clearly, however, this holds only for species–area relationships derived from nested sampling areas because of the assumption that $\log s_{max} = \log \gamma$. For the moth data, a $z = 0.578$ is required for $s_{max} = \gamma = 179$, which corresponds to the multiplicative partition of $\beta = \gamma/\alpha = 179/66.7 = 2.68$ (in units of community turnover). If the observed $z = 0.148$ is used, then $s_{max} = 90.5$ or $\beta = 90.5/66.7 = 1.36$. Thus, the observed slope of the species–area relationship for moths in isolated habitats underestimates the total β-diversity by 49% using a multiplicative definition, and 79% using an additive definition ($\beta_{area} = 23.8$ vs. $\beta = 112.3$ species).

A more detailed analysis of the moth data suggests that habitat heterogeneity, specifically differences in tree species diversity and composition, influence the moth species composition among habitats (Summerville & Crist 2004). Distance-dependent dissimilarity in species composition can also lead to high levels of β-diversity due to environmental variation or dispersal limitation (Condit *et al.* 2002; Martin *et al.* 2005; Qian *et al.* 2005). If habitat areas are small, stochastic sampling of the species pool may also result in weak dependence of species richness on area (Lomolino 2000) and would therefore produce a relatively large $\beta_{replace}$.

DISCUSSION

Additive partitions of diversity are increasingly used in the analysis of species diversity across multiple scales (Wagner *et al.* 2000; Gering & Crist 2002; Crist *et al.* 2003; Gering *et al.* 2003; Martin *et al.* 2005; Roschewitz *et al.* 2005; Summerville & Crist 2005). The need to test for the statistical significance of diversity components is clear because the observed α-, β-, and γ-components of diversity will always depend on the sample grain and extent of the study (Fig. 2). A relatively small α- and large β-component, for example, may be due to a fine sample grain (such as a 1-m^2 quadrat) combined with large numbers of samples collected from a large spatial extent. The null distributions in randomization tests (Crist *et al.* 2003) are based on the observed sample grain and extent, and therefore provide robust tests of whether the observed diversity partitions differ from those expected by chance. The emphasis on α- and β-components of diversity may help identify the contributions of study grain and extent to the sampled γ-diversity, just as others have demonstrated for species–area relationships derived from nested sampling areas (Palmer & White 1994; Leitner & Rosenzweig 1997; Crawley & Harral 2001; Arita & Rodríguez 2002). We have emphasized hierarchical sampling because diversity partitions may be applied to samples from quadrats, transects, or traps, but our approach is equally amenable to area-based sampling if hierarchical levels are reflected by sampling areas of increasing size. This is particularly evident in the relationships between average patch occupancy and additive

partitioning because incidence may be expressed as proportion of habitat or sampling area.

The observed components of α-, β- and γ-diversity have exact counterparts in the sample-based rarefaction curve, and the randomization test using random placement of individuals is an approximate counterpart to the individual-based rarefaction curve. Therefore, the analysis of hierarchical diversity partitions in PARTITION complements the widely used ESTIMATES software (Colwell 2004), which conducts sample-based and individual-based rarefaction as well as species-richness estimation. This linkage between additive diversity partitions and rarefaction provides a framework for the analysis of species diversity at multiple spatial and temporal scales. First, it suggests that the relative sizes of α-, β- and γ-components of diversity between different landscapes or regions may require rarefaction to standardize data to an equal sample size (Gotelli & Colwell 2001) or randomization tests that explicitly factor sample abundance into the test (Crist *et al.* 2003). Second, additive partitions of diversity may inform survey efforts aimed at estimating biodiversity because diversity components identify the spatial or temporal components of sampling that contribute most to γ, and therefore where additional sampling effort would yield the greatest increase in numbers of species (Stohlgren *et al.* 1997; Gimaret-Carpentier *et al.* 1998). For example, Summerville & Crist (2005) concluded from a 3-year moth survey of an old-growth deciduous forest that increased sampling effort among seasons yielded greater accumulation of new species than did additional years.

Additive partitioning does not provide estimates of the true species richness of a habitat or region. Partitions of γ- into α- and β-components, whether additive or multiplicative, are only as accurate as the estimates of α_i and γ. High levels of β-diversity may arise from the ecological effects of habitat heterogeneity and dispersal limitation (Condit *et al.* 2002; Cotennie 2005; Legendre *et al.* 2005; Crist *et al.* 2006), or from sampling effects where a portion of the α-diversity within habitats appears as β-diversity because of additional sampling effort among habitats (Lande 1996; Cam *et al.* 2002; Ugland *et al.* 2003; Colwell *et al.* 2004). Thus, although the γ-diversity in butterfly example was adequately sampled (49 of an estimated 51 species), the observed $\alpha = 16.7$ species may have been underestimated since the 13 patches with the largest sample sizes resulted in $\alpha = 19.6$ species (Fig. 2). If the α-component was underestimated by 2.9 species, then the true proportion of γ due to α would be 0.40 (instead of 0.34). Habitat heterogeneity also influenced the β-diversity of butterflies, however, since significant differences in host–plant composition occurred among habitats (data not shown). In the moth example, γ was underestimated (179 of an estimated 209 species), which suggests the α-component was likely underestimated as well. Assuming that all of the difference between the observed and estimated γ was due to undersampling within habitats, the α-component would change from $66.7/179 = 0.34$ to $97.7/209 = 0.46$. It is unclear how underestimation of α or γ would affect the relative size of β_{area} and $\beta_{replace}$ in the species–area relationship. Cam *et al.* (2002) used sight-resight probabilities with program CAPTURE (Otis *et al.* 1978) to estimate bird species richness from breeding-bird survey data. Comparisons of observed counts and estimated species richness as a function of sampling effort showed that the count data had a lower intercept and a steeper slope than the estimated richness (Cam *et al.* 2002). Applied to the additive partition of the species–area relationship, this implies that the α-component may be underestimated and the β_{area}-component overestimated by count data. In cases where richness is compared with area rather than sampling effort, however, the β_{area} could be underestimated if the difference between observed and true species richness is greater in larger habitats.

Several authors have related α- and β-components of species richness to parameters of the species–area relationship (Rosenzweig 1995; Hubbell 2001; Scheiner 2003). There are difficulties with this analogy, however. First, as we have shown, it assumes that all of the β-diversity is due to area alone; this is true only of species–area relationships derived from nested sampling areas (see also Wilson & Shmida 1984), or in the rare instance when species form perfectly nested subsets among isolated habitats (Wright *et al.* 1998). Shifts in species composition among isolated habitats are often unrelated to area, and may comprise a significant fraction, if not most, of the β-diversity (Fig. 3). Second, if nonlinear functions other than the power law are used to describe the species–area relationship, then β-diversity estimated from the slope has different units of community turnover that are not comparable among statistical models. Third, least-squares estimates of the slope, intercept, and asymptote (if present) are difficult to interpret independently, because all parameters together influence the overall shape of the curve (Connor & McCoy 1979; Tjørve 2003). Finally, it implies that there is no β-diversity present if species richness does not vary predictably with habitat area; indeed, many data sets show no significant species–area relationship (Connor & McCoy 1979; Drakare *et al.* 2006) yet may have high levels of β-diversity.

We provide a framework to partition the effects of habitat area on the total β-diversity, using either additive or multiplicative components of richness. The differences in total β and β_{area} can be expressed using the multiplicative definition of β if the multiplicative β-component is not equated with the slope of the species–area relationship. Since both additive and multiplicative components of β_{area} will differ with changes in the species–area relationship,

either measure could be used to detect changes in β and β_{area} across spatial scales. Additive partitioning of the species–area relationship uses the same units of species richness for both α- and β-diversity, which allows direct comparisons of α, β_{area} and $\beta_{replace}$ across scales. Our current approach has limitations, however. The estimation of the β_{area}-component using the predicted value of s_{max} from the largest habitat area may be problematic for some species–area relationships where very large habitat areas have a disproportionate effect on the species–area regression. We have found that estimation of β_{area} is robust to different functional forms of the species–area relationship (power, exponential, logistic, etc.) for most data sets. Nonetheless, better alternatives to estimating β_{area} might be developed in future studies. The partitioning of β_{area} and $\beta_{replace}$ also does not resolve the long-standing problem of whether changes in species richness are due to area *per se* or to the greater habitat diversity often found within larger habitats (Connor & McCoy 1979; Cam *et al.* 2002), but it does recognize that β-diversity occurs among habitats due to habitat heterogeneity or dispersal limitation (Scheiner 2003). In a recent meta-analysis of nearly 800 species–area data sets, Drakare *et al.* (2006) concluded that there is a need to integrate β-diversity with species–area relationships. The partitioning of the species–area relationship into different β-components of species richness is a step in this direction.

The relationships among additive partitioning, patch occupancy, rarefaction curves, and species–area relationships suggest a fertile common ground for quantifying and comparing α- and β-diversity in heterogeneous landscapes. A greater recognition of the linkages among additive diversity partitions may help to synthesize various approaches to analyzing and comparing species diversity, as well as lead to a greater understanding of how species diversity is influenced by spatial and temporal scales of sampling.

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