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A contribution diversity approach to evaluate species diversity

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Summary

Measuring species diversity is critical for ecological research and biodiversity conservation. The separate assessment of within-unit diversity and unit distinctiveness in the form of endemism may lead to biased results when evaluating the importance of a unit for regional diversity. In this paper, we adopt the additive partitioning of species diversity and propose a series of measurements decomposing the contribution of a unit into two components, one based on within-unit species diversity and the other on unit distinctiveness, for species richness and Simpson's index. We also propose a differentiation coefficient to evaluate the distribution of species diversity within and among units and to compare the relative importance of unit distinctiveness and within-unit diversity for regional diversity. Using simulations and a real data set of tree species in a community consisting of nine plots, we compared the proposed method with other ranking methods. The definition of unit-specific additive components of species diversity facilitates diversity scaling in hierarchical systems. The individual components may be used to identify the factors determining the contribution of a unit to larger-scale diversity, while avoiding typical problems associated with the number of endemic species. The ranking of units based on an integrated assessment of α and β diversity at the unit level provides an objective foundation for determining conservation priorities.

Zusammenfassung

Für ökologische Forschung und den Schutz der Biodiversität ist die Erfassung der Artendiversität entscheidend. Die getrennte Betrachtung der Diversität innerhalb

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einer Einheit und die Besonderheit der Einheit in Form von Endemismus kann zu einer Schiefe der Ergebnisse führen, wenn die Bedeutung einer Einheit für die regionale Diversität evaluiert wird. In dieser Veröffentlichung wenden wir die additive Partitionierung der Artendiversität an und schlagen eine Serie von Erfassungen vor, die den Beitrag einer Einheit am Artenreichtum und Simpsons Index in zwei Komponenten teilt, eine basiert auf der Artendiversität innerhalb der Einheit und die andere auf der Besonderheit der Einheit. Wir schlagen außerdem einen Differenzierungskoeffizienten vor, um die relative Bedeutung der Besonderheit einer Einheit und der Diversität innerhalb einer Einheit für die regionale Artendiversität zu evaluieren. Unter Verwendung von Simulationen und eines echten Datensatzes von Baumarten in einer Gemeinschaft, die aus neun Flächen besteht, verglichen wir die vorgeschlagene Methode mit den Rangfolgemethoden. Die Definition von einheitenspezifischen additiven Komponenten der Artendiversität ermöglicht die Einordnung in hierarchische Systeme. Die individuellen Komponenten können benutzt werden, um die Faktoren zu bestimmen, die den Beitrag einer Einheit zur Diversität auf einer größeren Skala bestimmen, wobei die typischen Probleme vermieden werden, die mit der Anzahl der endemischen Arten verbunden sind. Die Klassifizierung der Einheiten, die auf einer integrierten Einschätzung der α- und β-Diversität auf dem Einheitenlevel basiert, stellt ein objektives Fundament für die Bestimmung von Schutzprioritäten zur Verfügung.

Introduction

Measuring species diversity is critical for ecological research and biodiversity conservation. In the ecological literature, many measures have been proposed to assess species diversity based on data on presence or abundance of species (Magurran, 1988; Pielou, 1975). Because species diversity is unevenly distributed among units, the contribution of each unit to region-level diversity is not equal. Usually, the higher the contribution of a unit, the higher the priority it should receive from the biological view (Johnson, 1995).

In a region consisting of many units, the species diversity found in each unit, i.e., α diversity as defined by Whittaker (1960), is commonly used to rank the importance of each unit for the region. Species richness is the simplest and most frequently used diversity measure. However, species-richness assessments are notoriously sensitive to scale, due to the species–area relationship (Palmer & White, 1994; Veech, 2000), and to sampling effort, due to the difficulty of obtaining complete species lists (Palmer, 1995). The two problems are closely related: the number of observed species generally increases with the number of individuals sampled, and the number of individuals increases with the size of the sampling unit. In order to compare species richness among units of different size, the rarefaction method (Hurlbert, 1971) or Coleman's method (Coleman, 1981) can be used. Recently, Veech (2000) and Hobohm (2003) have shown how the residuals of species richness based on species–area curves can be used to rank units.

When the contribution of a unit is assessed from within-unit species diversity alone, differences in unit distinctiveness may introduce considerable bias. A unit that has many specialist species will contribute more to the regional species diversity than another unit with the same number of species, all of which are generalists (Wagner & Edwards, 2001). Unit distinctiveness is determined by the distinctiveness of each species in the unit. Species distinctiveness is essentially a continuum, with the highest values for endemic species that occur only in a single unit, and the lowest values for universal species occurring in every unit. Despite the continuous nature of distinctiveness, the binary definition of endemism is frequently used to assess unit distinctiveness from regional to global levels (Johnson, 1995; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000).

Because within-unit species diversity and distinctiveness are two different aspects of the contribution of a unit to regional species diversity, they should be combined in evaluating the contribution of a unit to higher-level species diversity. However, they are usually considered separately (Johnson, 1995; Myers et al., 2000; Hobohm, 2003). By extending Dufrene and Legendre's (1997) approach, Wagner and Edwards (2001) defined unit specificity as the sum of the specificity of each species, which is based on its frequency of occurrence among units. Although this seems to be a distinctiveness approach, the measure combines richness and distinctiveness (Wagner & Edwards, 2001). However, this measure cannot tell us which part, the richness or distinctiveness, plays the more important role for the contribution of a unit to the species diversity in the region. Furthermore, it cannot be simply extended and applied to Simpson's index or other species diversity measures.

Whittaker proposed scale-dependent species diversity terms, where among-unit diversity β is a dimensionless, multiplicative factor linking within-unit diversity α and regional diversity γ $(\gamma = \alpha \times \beta)$, In recent years, however, the additive partitioning of species diversity that expresses β in the same units as α and $\gamma(\gamma = \alpha + \beta)$ is increasingly applied in ecological research and biodiversity conservation (Lande, 1996; Veech, Summerville, Crist, & Gering, 2002), explicitly quantifying how γ diversity is partitioned into α and β diversity (Chen, Lu, Ying, & Song, 2006; Crist, Veech, Gering, & Summerville, 2003; Fournier & Loreau, 2001; Gering & Crist, 2002; Gering, Crist, & Veech, 2003; Loreau, 2000; Martin, Moloney, & Wilsey, 2005; Ricotta, 2003; Stendera & Johnson, 2005; Wagner, Wildi, & Ewald, 2000). The additive approach treats α diversity as the average within-unit diversity, regardless of whether diversity is measured by species richness or Simpson's index. Among-unit diversity β is thus the average amount of diversity not found in a single, randomly chosen unit (Veech et al., 2002), and reflects the distinctiveness of all units. Therefore, α and β diversity are commensurate and can directly be compared. If β diversity could be dissected and attributed to each unit, it would be easier to develop a combined index that integrates within-unit diversity and unit distinctiveness.

In the present paper, we derive methods to attribute an additive β diversity component to each unit by quantifying species and unit distinctiveness, and propose indices combining the two aspects of species diversity to evaluate the contribution of a specific unit to regional diversity. We develop the methods not only for species richness, but also for the Simpson's index, which incorporates the number and abundance of species. The calculations are illustrated with a small artificial data set, and the ranking method is evaluated with simulations using a real data set of plant diversity in Tiantong National Forest Park, Zhejiang Province of China.

Methods

According to the additive partitioning of species diversity, $\gamma = \alpha + \beta$, where α is the average within-unit diversity, and β is the average amount of diversity not found in a single, randomly-chosen unit (Lande, 1996; Veech et al., 2002). Obviously, γ is also an average; it is the average amount of the diversity each unit contributes to the region, which combines the within-unit diversity with the distinctiveness of each unit. This additive partitioning can be applied to multiple scales (Loreau, 2000) as well as to different diversity measures (Ricotta, 2005; Veech et al., 2002), including species richness, Simpson's index and Shannon information index (Veech et al., 2002). Symbols and their descriptions used in this study are listed in Table 1.

Species richness-based contribution diversity

Given a region that consists of a set of n units of equal size with complete species lists, we define region-level species richness γ_{ST} as the sum of the unit-level contributions α_{ST} and β_{ST} to the region, i.e. $\alpha_{ST} = \Sigma_k^n \alpha_{S(k)}$, $\beta_{ST} = \Sigma_k^n \beta_{S(k)}$, and $\gamma_{ST} = \Sigma_k^n \gamma_{S(k)} = \alpha_{ST} + \beta_{ST}$. Let S_k and S be the species richness of the kth unit and of the region, respectively, then

$$\alpha_{ST} = \frac{1}{n}\sum_k^n S_k = \frac{1}{n}\sum_i^S n_i,$$

where n_i is the number of units in which the ith species occurs within the region, and $\gamma_{ST} = S$. The contribution of the kth unit to the species richness of the region is

$$\alpha_{S(k)} = \frac{1}{n}S_k = \sum_i^{S_k}\frac{1}{n}.$$

According to the additive relationship, we can obtain the β diversity of the region as

$$\beta_{ST} = \gamma_{ST} - \alpha_{ST} = \sum_i^S \frac{n - n_i}{n}.$$

Obviously, $(n{-}n_i)/n$ represents the β diversity, i.e. distinctiveness or among-unit diversity, of the ith species and depends on the frequency of the species in the region. Therefore, for a specific unit with the ith species, the distinctiveness contributed by this species and unit is $(n{-}n_i)/nn_i$. As the number of units of the region is fixed, the fewer units the ith species appears in, the higher is the distinctiveness of each unit that contains the ith species. The distinctiveness of the kth unit can be obtained by summing the distinctiveness of all species, i.e.

$$\beta_{S(k)} = \sum_i^{S_k}\frac{n - n_i}{nn_i}.$$

Table 1. Symbols and their description used in the present study

Description	Species richness-based approach	Simpson's index-based approach
The number of units of the region	n	n
The number of units where the *i*th species occurs in the region	n_i	
The number of species of the *k*th unit	S_k	
The number of endemic species of the *k*th unit	S_{Ek}	
The number of species at the region level	S	
The number of endemic species at the region level	S_{E}	
The abundance of the *i*th species in the *k*th unit		$P_{i(k)}$
The abundance of the *i*th species among *n* units in the region		P_i
Simpson's index of the *k*th unit		$D_{(k)}$
The contribution of the *k*th unit to within-unit diversity	$\alpha_{S(k)}$	$\alpha_{D(k)}$
Distinctiveness or the contribution of the *k*th unit to among-unit diversity	$\beta_{S(k)}$	$\beta_{D(k)}$
The contribution to region-level species diversity	$\gamma_{S(k)}$	$\gamma_{D(k)}$
Within-unit diversity	α_{ST}	α_{DT}
Among-unit diversity	β_{ST}	β_{DT}
Species diversity at the region level	γ_{ST}	γ_{DT}
Differentiation coefficient	D_{ST}	D_{DT}
Relative contribution of the *k*th unit to within-unit diversity of the region	$C_{\alpha S(k)}$	$C_{\alpha D(k)}$
Relative distinctiveness of the *k*th unit or relative contribution of the *k*th unit to among-unit diversity of the region	$C_{\beta S(k)}$	$C_{\beta D(k)}$
Relative contribution diversity of the *k*th unit to the region	$C_{\gamma S(k)}$	$C_{\gamma D(k)}$

The contribution diversity of the *k*th unit to the region can thus be expressed by

$$\gamma_{S(k)} = \alpha_{S(k)} + \beta_{S(k)} = \sum_{i}^{S_k} \frac{1}{n_i}.$$

We define an estimator of within-region differentiation as $D_{ST} = \beta_{ST}/\gamma_{ST}$. A value of $D_{ST} > 0.5$ means that most diversity is distributed among units and high distinctiveness may play a key role in determining the contribution of units to the region.

We also define the relative contribution of the *k*th unit to within-unit (α), among-unit (β) and regional species richness (γ) as

$$C_{\alpha S(k)} = \frac{\alpha_{S(k)} - \bar{\alpha}_S}{\gamma_{ST}}, \quad C_{\beta S(k)} = \frac{\beta_{S(k)} - \bar{\beta}_S}{\gamma_{ST}}$$

and

$$C_{\gamma S(k)} = \frac{\gamma_{S(k)} - \bar{\gamma}_S}{\gamma_{ST}},$$

where $\bar{\alpha}_S = \alpha_{ST}/n$, $\bar{\beta}_S = \beta_{ST}/n$ and $\bar{\gamma}_S = \gamma_{ST}/n$ are the averages of within-unit diversity, among-unit diversity and contribution diversity of all units. Obviously, they have the following relationship: $C_{\gamma S(k)} = C_{\alpha S(k)}$+$C_{\beta S(k)}$.

Note that the values of $C_{\alpha S(k)}$, $C_{\beta S(k)}$ and $C_{\gamma S(k)}$ may be positive or negative, and the respective sums of $C_{\alpha S(k)}$, $C_{\beta S(k)}$ and $C_{\gamma S(k)}$ over all units *k* in the region are zero. A positive value means that the contribution of a specific unit to within-unit, among-unit or total species richness of the region is higher than the average of all units, whereas a negative value indicates a below-average contribution.

Simpson's index-based contribution diversity

Let $P_{i(k)}$ be the relative abundance of the *i*th species in the *k*th unit, and let P_i be the relative abundance of the *i*th species among *n* units in the region, i.e. $P_i = \Sigma_k P_{i(k)}/n$. Simpson's index of the *k*th unit is estimated by $\alpha_{D(k)} = 1 - \Sigma_i P_{i(k)}^2$, and that of the region is estimated by $\gamma_{DT} = 1 - \Sigma_i P_i^2 = 1 - \frac{1}{n}\Sigma_i \Sigma_k P_{i(k)} P_i$.

According to the additive relationship, the region-level species diversity is the average of the unit-level contribution to the region, so within- and among-unit diversity at the region level are obtained as $\alpha_{DT} = \frac{1}{n}\Sigma_k \alpha_{D(k)} = 1 - \frac{1}{n}\Sigma_i \Sigma_k P_{i(k)}^2$ and $\beta_{DT} = \gamma_{DT} - \alpha_{DT} = \Sigma_i \Sigma_k P_{i(k)}(P_{i(k)} - P_i)$. Obviously, $P_{i(k)}(P_{i(k)} - P_i)$ represents the contribution of the *k*th unit to among-unit diversity of the region for the *i*th species. Then the contribution of the *k*th unit can be obtained by summing the values of each component species, i.e., $\beta_{D(k)} = \Sigma_i P_{i(k)}(P_{i(k)} - P_i)$. Therefore, the contribution of the *k*th unit to the species diversity of the region can be estimated by $\gamma_{D(k)} = \alpha_{D(k)} + \beta_{D(k)} = 1 - \Sigma_i P_{i(k)} P_i$. A Simpson's index-based differentiation coefficient can be defined as $D_{DT} = \beta_{DT}/\gamma_{DT}$.

With these estimates, we can also characterize the relative contribution of the *k*th unit to within-unit, among-unit and total species diversity of the region by

$$C_{\alpha D(k)} = \frac{\alpha_{D(k)} - \bar{\alpha}_D}{n\gamma_{DT}}, \quad C_{\beta D(k)} = \frac{\beta_{D(k)} - \bar{\beta}_D}{n\gamma_{DT}}$$

and

$$C_{\gamma D(k)} = \frac{\gamma_{D(k)} - \bar{\gamma}_D}{n\gamma_{DT}}.$$

The ecological meanings of these components are the same as for the corresponding estimates in the species-richness approach.

Example data sets

An artificial data set

A simple example of three units (A, B and C), each containing three out of six species (a–f), illustrates the calculations (Table 2). Total species richness is $S = \gamma_{ST} = 6$, with $\alpha_{ST} = 3$ and $\beta_{ST} = 3$ (Table 2, top), and total Simpson diversity is $D = \gamma_{DT} = 22/27$, with $\alpha_{ST} = 2/3$ and $\beta_{ST} = 4/27$ (Table 2, bottom). Unit A is the most distinct with two endemic species, followed by unit C with one and unit B with no endemic species. This ranking is reflected in the units' contributions to β and γ diversity, with the highest values for unit A, both in terms of species richness and Simpson diversity.

Simulations

The behavior of the proposed ranking method was evaluated by simulating a set of sampling units that were expected to have the same contribution to α diversity, while they should differ systematically in their contributions to β diversity. A set of species with Gaussian abundance distributions (10, 20, 40 or 80 species) was modeled. Species optima were spaced equally along a gradient. The gradient was subdivided into 80 sampling units, and the ends of the gradient were joined in order to avoid edge effects. All species distributions had the same standard deviation or tolerance (2, 4 or 8 units). Sensitivity to the size of the sampling unit or sampling effort was assessed by manipulating the number of individuals. A fixed number of individuals (10, 20, 40 or 80) was sampled for each unit, with species probabilities proportional to the expected abundance in the respective unit. An initial pair of sampling units, separated by 3 units, was randomly chosen. Another eight units were selected with intervals of increasing size (5, 7, 9 and 11 units) in both directions from the two initially selected units, resulting in a maximum distance of 13 units between the last units from both sides. The larger the intervals on both sides of a unit, the higher its expected contribution to β diversity. There were always two units with the same distance configuration, so that these units were expected to have identical diversity components. A good ranking method should find an approximately linear correlation of the contribution to β and γ diversity with expected ranks, and similar values for units with the same expected rank.

Simulations were repeated 100 times for each combination of number of species, number of

Table 2. Artificial data set describing the occurrence of six species (a–f) in the three units (A–C), and selected diversity components for species richness (top) and for Simpson index (bottom)

$S_{i(k)}$	a	b	c	d	e	f	$S_{(k)}$	$\alpha_{S(k)}$	$\beta_{S(k)}$	$\gamma_{S(k)}$	$C_{\gamma S(k)}$
A	1	1	1				3	1	3/2	5/2	1/2
B			1	1	1		3	1	1/2	3/2	−1/2
C				1	1	1	3	1	1	2	0
							S	α_{ST}	β_{ST}	γ_{ST}	
Total	1	1	2	2	2	1	6	3	3	6	
$P_{i(k)}$	a	b	c	d	e	f	$D_{(k)}$	$\alpha_{D(k)}$	$\beta_{D(k)}$	$\gamma_{D(k)}$	$C\gamma_{D(k)}$
A	1/3	1/3	1/3				2/3	18/27	5/27	23/27	1/27
B			1/3	1/3	1/3		2/3	18/27	3/27	21/27	−1/27
C				1/3	1/3	1/3	2/3	18/27	4/27	22/27	0
							D	α_{DT}	β_{DT}	γ_{DT}	
Total	1/9	1/9	2/9	2/9	2/9	1/9	22/27	18/27	4/27	22/27	

individuals, and tolerance. After each replicate simulation, diversity components were calculated. Ranking performance was evaluated by the R^2 of linear regressions of the number of endemic species S_{Ek} and of the contributions to β and γ diversity, $\beta_{S(k)}$ and $\gamma_{S(k)}$, on the expected ranks.

A real data set

We illustrate the ecological application of the proposed methods with data from a *Castanopsis fargesii+Schima superba* community, the local climax vegetation type, in Tiantong National Forest Park (TNP), Zhejiang Province of China (Song & Wang, 1995). The community data (region) consisted of nine 400 m^2 plots (units) (see Appendix A). Each plot was further divided into sixteen $5 \times 5\,m^2$ subplots. Each individual with diameter at breast height >5 cm was recorded and measured. $P_{i(k)}$ was defined as the relative importance value, which is measured as one-third of the sum of the relative abundance, relative dominance and relative frequency, of species i in the pooled subplots of unit k.

Based on these data, we calculated α, β and γ diversity components for species richness and Simpson index using the proposed formulae. To compare with other measurements, we also calculated unit specificity, S_j^{aj} (total specificity of the unit j) and S_j (relative specificity of the unit j) (Wagner & Edwards, 2001) and residuals of species –area curves based on species richness (R_S) and endemic species (R_E), respectively (Hobohm, 2003). As all plots were of the same size, residuals were calculated as $\log S - \log S_{\text{mean}}$ for species richness and $\log E - \log E_{\text{mean}}$ for endemic species.

To evaluate the ranking of the units, we also applied the complementarity approach (Vane-Wright, Humphries, & Williams, 1991), which has been widely used to identify areas of conservation priority based on species richness. This is an iterative procedure that selects units in a stepwise manner, such that at each step the newly selected unit includes the greatest number of species not yet represented among selected units (Vane-Wright et al., 1991). All units are initially ranked according by the number of species, and the unit with the highest number of species is chosen first. Once the first choice has been made, all species included within that unit are ignored. The second area is then drawn from the taxonomic complement of the first–the unit with the highest number of remaining species. This algorithmic procedure is repeated until all species are accounted for the total complement (Vane-Wright et al., 1991).

Results

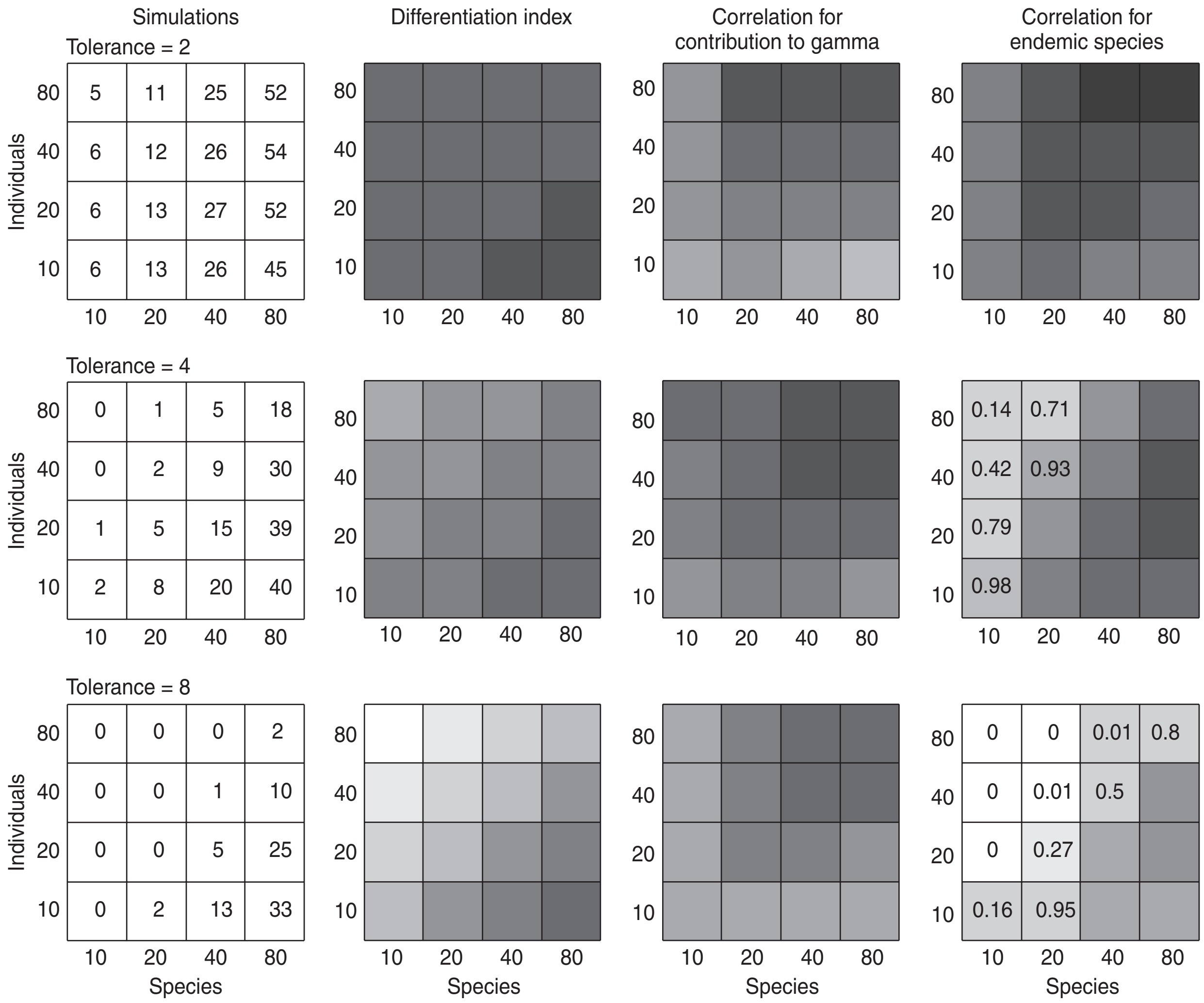
Simulation results

The sampled units differed much in species composition and little in species richness, so that $\gamma_{S(k)}$ was highly correlated with $\beta_{S(k)}$ ($r = 0.97$, only $\gamma_{S(k)}$ shown in Fig. 1, third column). The performance of the ranking methods depended strongly on species tolerance, i.e., the standard deviation of simulated species distributions (Fig. 1, with increasing tolerance from top to bottom row). As expected, the differentiation index (Fig. 1, second column) decreased with increasing tolerance, due to an increasing overlap of species abundance distributions along the gradient. However, small samples from species communities artificially increased D_{ST}. Narrow speciose distributions (Fig. 1, top row) resulted in high numbers of endemic species, leading to generally high linear correlations between the expected ranks and all three diversity measures. S_{Ek} (Fig. 1, last column) performed slightly better than $\gamma_{S(k)}$, mostly because the latter was more sensitive to sample size. On the other hand, $\gamma_{S(k)}$ was robust towards changes in tolerance, whereas the performance of S_{Ek} decreased strongly with increasing tolerance, especially for large samples and few simulated species. Furthermore, S_{Ek} often could not be calculated at all in these situations.

Tiantong National Forest Park data

In the nine plots (units) of the *Castanopsis fargesii+Schima superba* community (region), γ diversity was 42, means of α and β diversity were 13.22 and 28.78, respectively, based on species richness (Table 3). The differentiation index was $D_{ST} = 0.685$, indicating that most diversity was partitioned among units. Relative contributions of five units (T11, T21, T34, T01, and T40) were positive, indicating that their contributions were larger than the average. Relative contribution diversity ($C_{\gamma S(k)}$) was significantly correlated with relative unit distinctiveness ($C_{\beta S(k)}$) ($P<0.01$) and had a critically significant correlation with the relative contribution of within-unit diversity ($C_{\alpha S(k)}$) ($P<0.10$) (Table 4). No significant correlation was found between relative contribution of within-unit diversity ($C_{\alpha S(k)}$) and relative unit distinctiveness ($C_{\beta S(k)}$).

The average of Simpson's indices of the units was 0.816, while Simpson's index of the region was 0.883. The differentiation index was $D_{DT} = 0.077$, indicating that most diversity was partitioned



Tolerance = 2

Individuals	10	20	40	80
80	5	11	25	52
40	6	12	26	54
20	6	13	27	52
10	6	13	26	45

Tolerance = 4

Individuals	10	20	40	80
80	0	1	5	18
40	0	2	9	30
20	1	5	15	39
10	2	8	20	40

Tolerance = 8

Individuals	10	20	40	80
80	0	0	0	2
40	0	0	1	10
20	0	0	5	25
10	0	2	13	33

Figure 1. Performance of ranking methods. Each cell shows the mean number of endemic species per simulation (left), the mean differentiation index D_{ST} (second column), or the mean correlation of $\gamma_{S(k)}$ (third column) or of S_{Ek} (right) with expected ranks, for a given combination of number of simulated species, number of individuals sampled from each unit, and species tolerance, averaged over 100 replicate simulations. Darker cells indicate higher values, so that the range from white to dark gray corresponds to a range of 0.4–1 for D_{ST} and 0–1 for the correlations. For S_{Ek}, numbers indicate the proportion of replicate simulations for which performance could be evaluated, if different from 1.

within units. Relative contributions of six units (T11, T40, T26, T21, T09 and T34) were positive (Table 3). Relative contribution diversity ($C_{\gamma D(k)}$) was positively correlated with the relative contribution to within-unit diversity ($C_{\alpha D(k)}$) ($P<0.01$) (Table 4), but negatively correlated with the relative contribution to among-unit diversity ($C_{\beta D(k)}$) ($P<0.01$) (Table 4).

Wagner and Edwards (2001) habitat specificity (S_j^{aj}) of each unit was identical to $\gamma_{S(k)}$, with unit T11 being the highest and the relative specificity of units ranging from 0.081 to 0.164 (Table 3). Habitat specificity also had a significant correlation with unit contribution diversity based on Simpson's index ($P<0.05$) (Table 4). Based on Hobohm's (2003) methods, residual values of five units were positive using species richness (R_S), and those of four units were positive using endemic species (R_E), assuming all the species were endemic to the sample collection. There were great differences in the results between the two residual approaches. Unit T21 had the highest number of species and its residual of the species–area curve was largest, but it had no endemic species. For this data set, due to equal area of the units, the residual of the species–area curve was a transformation of species richness and the correlation coefficient was 1 (Table 4). Because the residual of the endemic species–area curve (R_E) estimated the distinctiveness of endemic species, it had a significant correlation with unit distinctiveness ($C_{\beta S(k)}$) ($P<0.01$) (Table 4). It was also significantly

Table 3. Species diversities estimated by different measurements of nine plots of *Castanopsis fargesii*+*Schima superba* community in Tiantong National Forest Park, Zhejiang Province of China

	T01	T09	T40	T26	T11	T21	T15	T34	T18	Total
Species richness-based contribution diversity approach										
S_k	10	10	14	14	16	18	12	14	11	13.22
S_{Ek}	4	2	2	1	4	0	1	3	3	20
$\alpha_{S(k)}$	1.11	1.11	1.56	1.56	1.78	2.00	1.33	1.56	1.22	13.22
$\beta_{S(k)}$	3.78	2.28	3.15	2.73	5.12	3.12	1.87	3.56	3.17	28.78
$\gamma_{S(k)}$	4.89	3.39	4.70	4.29	6.89	5.12	3.20	5.12	4.39	42.00
$C_{\alpha S(k)}$ (%)	−0.85	−0.85	0.21	0.21	0.73	1.26	−0.32	0.21	−0.59	0.00
$C_{\beta S(k)}$ (%)	1.39	−2.18	−0.12	−1.11	4.57	−0.19	−3.16	0.87	−0.06	0.00
$C_{\gamma S(k)}$ (%)	0.54	−3.03	0.09	−0.91	5.30	1.08	−3.49	1.08	−0.65	0.00
Simpson's index-based contribution diversity approach										
$\alpha_{D(k)}$	0.745	0.822	0.826	0.887	0.886	0.876	0.605	0.860	0.831	0.816
$\beta_{D(k)}$	0.106	0.070	0.073	0.011	0.044	0.021	0.219	0.027	0.040	0.068
$\gamma_{D(k)}$	0.852	0.892	0.899	0.898	0.930	0.897	0.824	0.887	0.871	0.883
$C_{\alpha D(k)}$ (%)	−0.88	0.09	0.13	0.90	0.89	0.76	−2.65	0.56	0.20	0.00
$C_{\beta D(k)}$ (%)	0.48	0.03	0.06	−0.72	−0.30	−0.59	1.90	−0.51	−0.35	0.00
$C_{\gamma D(k)}$ (%)	−0.40	0.11	0.20	0.19	0.59	0.17	−0.75	0.05	−0.16	0.00
Other measurements										
S_j^{aj}	4.89	3.39	4.70	4.29	6.89	5.12	3.20	5.12	4.39	42.00
S_j	0.116	0.081	0.112	0.102	0.164	0.122	0.076	0.122	0.105	0.999
R_S	−0.121	−0.121	0.025	0.025	0.083	0.134	−0.042	0.025	−0.080	0
R_E	0.255	−0.046	−0.046	−0.347	0.255	−*	−0.347	0.130	0.130	0

S_j^{aj} – The total specificity of the unit *j* (Wagner & Edwards, 2001); S_j – The relative specificity of the unit *j* (Wagner & Edwards, 2001); R_S – Residual of species–area relationship based on species richness (Hobohm, 2003); R_E – residual of species–area relationship based on endemic species (Hobohm, 2003).

*The residual was not available because it had no endemic species.

Table 4. Correlation matrix between the parameters for nine plots of *Castanopsis fargesii*+*Schima superba* community in Tiantong National Forest Park, Zhejiang Province of China

	$C_{\alpha S(k)}$	$C_{\beta S(k)}$	$C_{\gamma S(k)}$	$C_{\alpha D(k)}$	$C_{\beta D(k)}$	$C_{\gamma D(k)}$	S_j^{aj}	S_j	R_S
$C_{\beta S(k)}$	0.37								
$C_{\gamma S(k)}$	0.60	0.97**							
$C_{\alpha D(k)}$	0.51	0.51	0.58						
$C_{\beta D(k)}$	−0.44	−0.44	−0.50	−0.98**					
$C_{\gamma D(k)}$	0.59	0.59	0.67*	0.90**	−0.79**				
S_j^{aj}	0.60	0.97**	1.00**	0.58	−0.50	0.67*			
S_j	0.60	0.97**	1.00**	0.59	−0.51	0.67*	1.00**		
R_S	1.00**	0.36	0.59	0.50	−0.43	0.58	0.59	0.59	
R_E	−0.02	0.80**	0.70*	0.35	−0.34	0.31	0.67*	0.67*	−0.05

*$P<0.05$; **$P<0.01$.

correlated with unit specificity and species richness-based contribution diversity ($P<0.05$) (Table 4).

Using the complementarity approach, biodiversity ranks were T21 > T11 > T34 > T01 > T18 > T09 = T40 > T15 = T26. Wagner and Edwards (2001) habitat specificity (S_j^{aj}) and the species richness–based contribution diversity ($\gamma_{S(k)}$) provided identical rank orders that were quite similar to the complementarity approach (Fig. 2), with a correlation of 0.90. The rankings based on residuals of the species–area curve (R_S) and residuals of the endemic species–area curve (R_E) differed considerably from the complementarity approach (correlations of 0.47 for R_S and 0.34 for R_E). Based on Simpson's index, contribution diversity ($\gamma_{D(k)}$) resulted in a rather different ranking (correlation with comlementarity: 0.27).

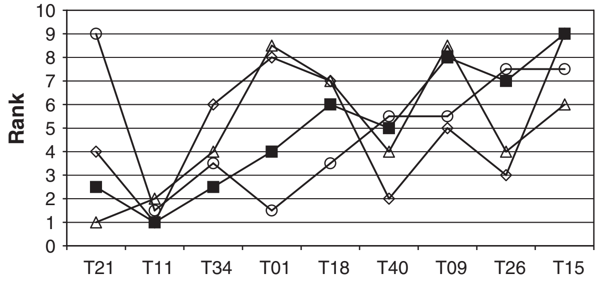


Figure 2. Ranking of the nine plots from the *Castanopsis fargesii+Schima superba* community in Tiantong National Forest Park, Zhejiang Province of China, according to the contribution to γ diversity based on species richness ($C_{\gamma S(k)}$: filled squares) and Simpsons index ($C_{\gamma D(k)}$: diamonds), residuals of species richness (R_S: triangles) and from of endemic species (R_E: circles). Plots were arranged according to the complementarity approach.

Discussion

The present paper defines the contribution of a unit to the biodiversity of the higher level, i.e. region, based on two aspects: the biodiversity found in the unit and the distinctiveness to the higher level. However, the two aspects were usually considered separately, which may lead to biased results. We defined species and unit distinctiveness based on the β diversity of additive partitioning and proposed measurements combining the two aspects of biodiversity to evaluate the contribution of a unit to the region. The contribution diversity proposed in this paper has three advantages. First, we can evaluate the contribution of each unit to the average α diversity or to the β diversity of the region. For instance, if some units have high α diversity while others have high distinctiveness, they may meet different conservation aims. For saturating local-regional richness curves, γ diversity increases because β diversity increases (Loreau, 2000). Therefore, with increasing number of units sampled, unit distinctiveness may become more important to determine contribution of each unit. In such case, a unit with more endemic species has a high rank for biodiversity management.

Secondly, contribution diversity defines α diversity and β diversity in commensurate measurement units. Ranking sampling units to determine conservation priority is a key issue for conservationists and biodiversity managers. Although, it has been acknowledged that both within-unit diversity and distinctiveness are important, usually they were separately used in setting conservation priorities (Johnson, 1995; Myers et al., 2000). To adjust the area effect, the residuals of species–area curves for species and endemic species had been proposed (Hobohm, 2003). However, these measurements may yield biased results. If α diversity and distinctiveness are assessed separately, it is difficult to decide which unit plays the more important role. For example, for the real data set in the present study, plot T21 had highest species richness, and thus had highest residuals in the species–area curve. However, because of the lack of endemics, its residual of the endemic species–area curve could not be determined (Table 4). Such results make decisions difficult.

Thirdly, the proposed methods evaluate unit distinctiveness based on the distinctiveness of all species in the unit, not only of the endemic species. Although, endemism has highest distinctiveness, other rare species may play key roles in the unit distinctiveness due to their large numbers. Furthermore, endemism is more dependent on the size of the sampling unit and may destroy the comparison base. A species may not be counted as endemic within a small area, but can become endemic if a larger area is considered. If the surface of the earth is considered as the study area, then all species are endemic (Hobohm, 2003). Distinctiveness is estimated according to the distribution range of each species, and species distinctiveness is a continuum, being 1 when it is an endemic species and 0 when it is distributed in all units. Therefore, using distinctiveness of all species might avoid problems of scale in defining endemism. Contribution diversity thus integrates unit specificity defined by Wagner and Edwards (2001) and the additive partitioning of species richness but can also be applied to Simpson's diversity index.

Wagner and Edwards (2001) found that unit specificity, which is equal to contribution diversity $\gamma_{S(k)}$, is much more robust towards sample size than species richness, especially when using stratified sampling. Our simulations suggest that the sensitivity of contribution diversity ($\gamma_{S(k)}$) to the number of individuals, which will depend on the size of the sampling unit and on sampling effort, was far less important than the effect of species tolerance on the number of endemic species (R_E). It is important to note, however, that these results assume that all units are equal in terms of size and sampling effort. For instance, simulations were repeated with varying number of individuals, but within each simulation run, this number was the same for all sampling units. Further research will need to assess the bias invoked by differences in size or sampling effort between sampling units and develop corrections, e.g., based on stratification or rarefaction methods.

Because contribution diversity can be dissected into two parts: contribution to α and β diversity, the relative significance of α and β diversity depends on the distribution of diversity. If more diversity was found among units, β diversity plays a more important role than α diversity does, and vice versa. This would mean that the ratio of α to β diversity would decrease as the size of sampling units increases. This problem is inherent to all methods comparing diversity components, because α diversity is a saturating function of γ diversity (Loreau, 2000). Our simulations suggest that in contrast to the number of endemic species, contribution diversity is quite robust towards the size of sampling units. The differentiation index was sensitive to the size of the sampling units, but in a different way than the number of endemics. With increasing species tolerance and decreasing β diversity, the differentiation index performed well for large samples of few species and was inflated for small samples from species-rich communities. This behavior suggests a sensitivity to stochastic effects of small samples. The number of endemics, in contrast, performed better for smaller samples of species communities but badly for species-poor communities, especially in the case of large samples. This reflects a lack of sensitivity in cases where most or all species occur in more than one unit, which is further aggravated by the problem that the residuals from the endemic species - area curve are not defined for units without endemic species.

Application to the Tiantong forest data suggested that richness-based contribution diversity provides results similar to the heuristic complementarity approach of Vane-Wright et al.(1991). Although the contribution diversity of each unit based on species richness and Simpson's index was significantly related (Table 4), they produced different rankings of the units (Table 3). Contribution diversity based on species richness was significantly correlated with unit distinctiveness, while based on Simpson's index, it was positively correlated with within-unit diversity and negatively correlated with unit distinctiveness. These differences were due to the fact that the species-richness approach is only based on species number, while Simpson's index approach also considers the relative abundance of each species. Therefore, results based on the two approaches may be different, as observed in α diversity from a variety of systems (Moyer, Riegl, Banks, & Dodge, 2003; Onaindia, Dominguez, Albizu, Garbisu, & Amezaga, 2004; Song & Wang, 1995). In fact, most of the diversity was partitioned within units using Simpson's index ($D_{DT}<0.5$), while most were partitioning among units using species richness ($D_{ST}>0.5$). A similar situation was observed in other studies on additive partitioning of species diversity (Wagner et al., 2000; Gering et al., 2003).

In the present study we proposed an example involving two hierarchical levels, where all units belong to the same type. The methods can also be applied to multiple levels. If there are different types, either diversity can be calculated first for each type and then for different types, or the units can be grouped and combined according to the type and then diversity calculated based on the types. Then α, β and γ diversity can be estimated level by level, as described by Crist et al. (2003) and Gering et al. (2003), with γ diversity of the lower level corresponding to the α diversity of higher level.

Our models are only based on species richness or the integration of species richness and species relative abundance, irrespective of the among-species differences such as taxonomic or genetic differences proposed by some authors (Vane-Wright et al., 1991; Faith, 1992; Hacker, Cowlishaw, & Williams, 1998). However, this aspect can also be added to our models by linking ecological diversity and biological diversity (Ganeshiaiah, Shekara, & Kumar, 1997; Ricotta, 2002).

While many studies report additive partitioning of diversity in a descriptive manner, Crist et al. (2003) stressed the importance of hypothesis testing and developed randomization tests for additive diversity components under two different null hypotheses. Under the null hypothesis of random species distributions, individuals are permuted among units many times in order to derive a null distribution for each diversity component. The procedure can easily be extended to the unit-specific components (e.g., $\alpha_{S(k)}$, $\beta_{S(k)}$) or the differentiation coefficients (D_{ST}, D_{DT}) defined here. An overall test for differences among units in their contribution to regional diversity could be based, for example, on the sum of the squared relative contributions $C_{\gamma S(k)}$. While the development of such tests may be straightforward for count data, appropriate permutation tests still need to be developed for compositional data, such as plant cover estimates.

Conclusions

This paper defined unit-specific additive components of species diversity that facilitate the scaling of species richness and Simpson index in hierarchical systems. It thus becomes possible to investigate which factors determine the contribution of a unit, landscape element or habitat type to larger-scale diversity, while avoiding typical problems associated with analysis based on the number of endemic species. The integrated assessment of α and β diversity at the unit level provides an objective ranking of units to support decision making in conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2006.06.004

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