

Comparison of phylobetadiversity indices based on community data from Gutianshan forest plot

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Phylobetadiversity incorporates phylogenetic information and beta diversity, and can account for the ecological similarities between communities with a phylogenetic perspective. Although different phylobetadiversity indices reflect differences in different characteristics between communities, the results of different phylobetadiversity indices are not comparable. In this study we examined phylobetadiversity indices for a 24-hm² plot in the Gutianshan National Nature Reserve. It was found the abundance-weighted D_{pw} was almost identical to Rao's D of Rao's quadratic entropy. PhyloSor had a similar ecological meaning and algorithm to UniFrac. Although D_{nn} was different in definition from UniFrac and PhyloSor, they were all strongly correlated. The effect of species abundance on phylobetadiversity was not significant when scales were relatively small, but was significant at larger scales. These contrasts likely resulted from reductions in evenness in communities as scales increased. P_{ST} and Rao's H better reflected the distance-decay changes caused by spatial and habitat variation than other indices at larger scales, whereas $AW-D_{nn}$ and D_{nn} better reflected these changes at small scales.

Scale, abundance, correlation, spatial pattern, distance decay

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Beta diversity is generally defined as the change in community composition along environmental gradients [1,2]. Because it directly links local diversity (alpha diversity) with regional diversity (gamma diversity), beta diversity is currently an important topic in community ecology [1,2]. Studies on the relationships between beta diversity and species characteristics, habitat gradients and limitations to seed dispersal can explain the mechanisms shaping patterns of beta diversity and test ecological hypotheses regarding the effects of regional diversity on local diversity [3,4].

Recently, the consideration of phylogenetic relationships among the species making up a community has provided new insights into community ecology [5]. Based on species

beta diversity, phylobetadiversity is defined as the phylogenetic distance among species or individual organisms of different communities [6]. Species beta diversity can be used to describe the dissimilarity of species composition among communities, but it is uninformative about the dissimilarity of phylogenetic relationships among communities [7,8]. For example, for 4 forest communities A, B, C and D located at different latitudes, all dissimilarity indices of species beta diversity between the forests of 1 means the species composition is completely different. However, the phylobetadiversity among these 4 communities may be dissimilar to different extents according to the relatedness of the communities.

Phylobetadiversity has been of considerable interest because of the potential new insights into community ecology

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it provides. A variety of definitions of phylobetadiversity and associated phylobetadiversity indices have been put forward. For example, D_{pw} is the mean pairwise phylogenetic distance of species or individuals among communities [9]; PhyloSor is defined as the proportion of branch length of shared species relative to total branch length of all species in two communities [10]; and PCD is defined as the extent to which the variance of a randomly selected trait in one community can be predicted by the value of the same trait in another community [11]. Presently, about 12 phylobetadiversity indices have been proposed. These indices can reflect dissimilarities among communities from different aspects, but the results using different indices are unlikely to be comparable.

The main ecological processes structuring the patterns of phylobetadiversity include niche-based deterministic and dispersal-based neutral models [6]. Niche-based deterministic models assume that phylobetadiversity patterns are determined by habitat heterogeneity and interspecific trade-offs in resource utilization, whereas dispersal-based neutral models hypothesize that phylobetadiversity patterns are shaped by spatial community dynamics, such as dispersal limitation [6]. Which of these indices can better reflect the changes in phylogenetic community structure along spatial and habitat gradients? So far, no studies have compared the characteristics of different phylobetadiversity indices.

This study aimed to compare properties of different phylobetadiversity indices using community data and environmental data from a 24-hm² forest dynamic plot in the Gutianshan National Nature Reserve. The Gutianshan Reserve is ideal to conduct such a comparative study. Previous studies on subtropical evergreen broad-leaved forests in the Gutianshan reserve found that both niche and spatial processes have similar effects (30% vs. 29%) on species beta diversity [12]. Moreover, the soil nutrients and species distribution have been mapped in the reserve at high resolution.

Based on the data from the Gutianshan plot, we aimed to address 4 questions: (1) Do phylobetadiversity indices, integrated with phylogenetic information, differ from species beta diversity indices? (2) Are phylobetadiversity indices correlated with each other, and do they have similar ecological meaning? (3) Does the effect of abundance-weighting on indices of phylobetadiversity vary with scale? (4) Can these indices reflect the phylobetadiversity along spatial and habitat gradients?

1 Materials and methods

1.1 Study site

The Gutianshan subtropical evergreen broad-leaved forest dynamic plot is located in the Gutianshan National Natural Reserve in Kaihua County, Zhejiang Province, China (29°10'19.4"~29°17'41.4"N, 118°03'49.7"~118°11'12.2"E). The total area of the reserve is 8107 hm² and its topography

is complex. The climate belongs to the middle subtropical monsoon climate zone, where the mean annual temperature is 15.3°C, mean hottest month temperature is 28.9°C and mean coldest month temperature is 4.1°C. With 140-d precipitation, the annual precipitation is 1963.7 mm. The area experiences, on average, 1747.5 sunshine hours and a 250-d frost-free season every year [13]. The Gutianshan forest plot is 600 m long and 400 m wide, and the altitude above sea ranges from 446.3 to 714.9 m. The plot was established in 2005 following the Center for Tropical Forest Science census protocol [14].

1.2 Reconstruction of community phylogeny

We reconstructed community phylogenies following Kress et al. [15] by sequencing 3 chloroplast DNA regions (*rbcLa*, *matK* and *trnH-psbA*) of 156 woody species growing in the plot. Total DNA was extracted from leaf tissue of plant samples using the CTAB method [16,17]. The 3 chloroplast DNA regions were amplified and sequenced, and the nucleotide sequences were aligned using MUSCLE [18]. The three regions were assembled into a supermatrix using R package phylotools [19]. Three-partition GTR + GAMMA models were applied to the 3 regions separately using RAxML [20] and a community phylogeny was constructed using maximum likelihood analysis. A bootstrap analysis with 1000 replicates was conducted to assess the percentage support for each node. Finally, an ultrametric tree was obtained using the non-parametric rate smoothing approach in the r8s software package [15,21,22].

1.3 Data analysis

Community data was obtained from the first survey of the Gutianshan 24 hm² forest plot. The survey covered 140700 woody plant individuals with diameter at breast height (dbh) ≥1 cm that belonged to 49 families, 104 genera and 159 species. The most abundant species were *Castanopsis eyrei* and *Schima superba*. We divided the 24-hm² plot into 600 20 m × 20 m, 150 40 m × 40 m, and 24 100 m × 100 m separate samples.

First, we conducted a Spearman correlation analysis of the 12 phylobetadiversity indices at the same spatial scale. Then we tested for correlations at 4 spatial scales between the 3 pairs of indices (D_{pw} vs. $AW-D_{pw}$, D_{nn} vs. $AW-D_{nn}$, and Π_{ST} vs. P_{ST}) in which each pair differed by whether or not it was abundance-weighted. Finally, we ran a Partial Mantel test with the phylobetadiversity indices values and spatial distance and/or environmental distance to compare the extent that the variation of phylobetadiversity caused by spatial and environmental distance could be explained by the different indices.

The environmental variables included four topographic

factors (mean elevation, convexity, slope, and aspect) [12] and 20 soil factors (total C, total N, total P, extractable Fe, extractable Mn, extractable Zn, extractable Cu, extractable K, extractable P, extractable Ca, extractable Mg, extractable Na, extractable B, extractable Si, extractable Al, extractable N, pH, N mineralization rate, bulk density, and soil moisture). Topographic factors can reflect soil moisture and nutrients indirectly. Because species in different conditions of soil moisture and nutrition have different competitive abilities, soil moisture and nutrition can affect the distribution of plants directly, so we used topographic and soil factors to represent ecological niche processes and spatial distance to represent spatial processes. According to geostatistical methods [23], we conducted soil sampling in 30 m × 30 m grids at different scales and standardized the measured factors with different methods depending on their attributes: pH values of every sample were standardized, the other soil factors were log-transformed, aspects of samples were transformed with sin(aspect) and cos(aspect) values to represent the extent of aspects facing south and east, and the other topographic factors were standardized with the same method as soil pH values.

We conducted principal component analysis (PCA) to determine the extent of variables that contributed to the principal components. The first principal component, in which mean elevation was the most important contributing variable, explained 92.9% of the information. The loading matrix of the environmental factors of the PCA is presented in Table S1. Thus we used the values for the first axis of every sample to represent habitat factors when calculating environmental distance between samples. Finally, we applied variance partitioning to phylobetadiversity values with spatial distance and/or environmental distance.

1.4 Phylobetadiversity indices

(i) D_{pw} . D_{pw} calculates the mean pairwise phylogenetic distance of different species or individuals among communities [9]. The algorithms are

$$D_{pw} = \frac{\sum_{i=1}^{n_{k_1}} \overline{\delta_{ik_2}} + \sum_{j=1}^{n_{k_2}} \overline{\delta_{jk_1}}}{n_{k_1} + n_{k_2}},$$

$$AW-D_{pw} = \frac{\sum_{i=1}^{n_{k_1}} f_i \overline{\delta_{ik_2}} + \sum_{j=1}^{n_{k_2}} f_j \overline{\delta_{jk_1}}}{2}, \text{ species } i \neq \text{species } j,$$

where $\overline{\delta_{ik_2}}$ is the mean pairwise phylogenetic distance between species i in community k_1 and all species in community k_2 ; n_{k_1} represents the number of species in community k_1 ; f_i is the relative abundance of species i in community k_1 [24]; and $AW-D_{pw}$ is the abundance-weighted D_{pw} .

(ii) D_{nn} . D_{nn} is defined as the mean phylogenetic distance between a species in community A and its most-

related species in community B [9]. The formulas are

$$D_{nn} = \frac{\sum_{i=1}^{S_A} \min \delta_{iB} + \sum_{j=1}^{S_B} \min \delta_{jA}}{S_A + S_B},$$

$$AW-D_{nn} = \frac{\sum_{i=1}^{S_A} f_i \min \delta_{iB} + \sum_{j=1}^{S_B} f_j \min \delta_{jA}}{2},$$

species $i \neq$ species j ,

where S_A is the number of species in community A ; $\min \delta_{jA}$ represents the phylogenetic distance between species j in community B and its closest relative species in community A ; f_i is the relative abundance of species i in community A [24,25]; and $AW-D_{nn}$ is the abundance-weighted D_{nn} .

(iii) PhyloSor. PhyloSor (Phylogenetic Sørensen index) is the proportion of branch length between shared species to total branch length of all species in two communities. As indicated in the name of this index, PhyloSor is a derivative of the Sørensen index (Sor), which is the proportion of shared species in relation to the total number of species in the communities. The larger the Sørensen value, the more similar the species composition is among communities; a larger PhyloSor value indicates closer community relationships. PhyloSor and Sørensen values are calculated by the formulas:

$$\text{Sor}_{ij} = \frac{2 \times S_{ij}}{S_i + S_j},$$

$$\text{PhyloSor}_{ij} = \frac{2 \times BL_{ij}}{BL_i + BL_j},$$

where S_{ij} is the number of species shared by two communities; S_i is the total number of species in community i [26]; BL_{ij} represents branch length between species shared by two communities; and BL_i is the branch length between all species of community i [10].

(iv) UniFrac. UniFrac (unique fraction) is defined as the percentage of branch length between species unique to one community [27]. The Jaccard index [1], which is similar to UniFrac, is an index of species beta diversity. Formulas for these two indices are

$$\text{Jaccard} = \frac{b + c}{a + b + c},$$

$$\text{UniFrac} = \frac{B + C}{A + B + C},$$

where a is number of shared species between communities; b is number of species unique to community 1; c is number of species unique to community 2; A represents branch length between species shared by the two communities; B represents branch length of species unique to community 1; and C represents branch length of species unique to community 2. UniFrac and PhyloSor have similar ecological meanings; the only difference is that the former is an index of dissimilarity between communities, whereas the latter is an index of similarity.

(v) Rao's D . Rao's D has the same meaning as AW- D_{pw} . It is computed as

$$D_{kl} = \sum_i \sum_j t_{ij} x_{ki} x_{lj},$$

where x_{ki} is relative abundance of species i in community k ; and t_{ij} represents phylogenetic distance between species i and j [28].

(vi) Rao's H . Rao's H is an index of phylogenetic diversity without consideration of the effect of phylogenetic diversity within communities. The formula is

$$H_{kl} = D_{kl} - (D_{kk} + D_{ll}) / 2,$$

where D_{kl} is the mean pairwise phylogenetic distance between communities; and D_{kk} and D_{ll} are the mean pairwise phylogenetic distances within communities k and l , respectively.

(vii) Π_{ST} and P_{ST} . Π_{ST} is calculated as the mean pairwise phylogenetic distance among communities minus the mean pairwise phylogenetic distance within communities. Π_{ST} only uses (0, 1) data, whereas P_{ST} contains species abundance information [8]. The indices are calculated by

$$\Pi_{ST} = \frac{\Delta_T^p - \Delta_S^p}{\Delta_T^p},$$

$$P_{ST} = \frac{D_T^p - D_S^p}{D_T^p},$$

where Δ_T^p is total phylogenetic diversity among all communities that can be understood as phylogenetic γ diversity; Δ_S^p represents the mean value of phylogenetic diversity within communities that can be understood as phylogenetic alpha diversity; and D_T^p and D_S^p are abundance-weighted phylogenetic gamma and alpha diversity, respectively.

(viii) PCD. PCD (phylogenetic community dissimilarity) can be broken up into a non-phylogenetic component (PCD_c), which reflects shared species among communities, and a phylogenetic component (PCD_p), which reflects relatedness of different species among communities. Interpretation of this phylogenetic beta diversity required the assumption that the evolutionary process of a non-selected trait is random, which is Brownian motion. Given the phylogenetic relationship between two communities, PCD represents the extent that variance of the trait in community 1 can be predicted by the same trait value in community 2:

$$PCD = \frac{n_1 PSV_{1|2} + n_2 PSV_{2|1}}{n_1 PSV_1 + n_2 PSV_2} \times \frac{1}{D(n_1 \times n_2 \times C_{pool})},$$

where n_1 means species number in community 1; $PSV_{1|2}$ represents the variance of the trait among species in community 1 given the trait variance in community 2 [29]; PSV_1 is the variance of the trait among species in community 1;

and $\bar{D}(n_1 \times n_2 \times C_{pool})$ is used to remove the deviation caused by n_1, n_2 [11].

2 Results

2.1 Correlations between indices

We investigated correlations between phylobetadiversity indices caused by the integration of phylogenetic information with species beta diversity using Spearman correlation analysis between UniFrac and PhyloSor, UniFrac and Jaccard [1], and PhyloSor and Sørensen [26]. These three pairs of indices have similar ecological meaning. Results at different spatial scales are shown in Table 1. Because Sørensen and Jaccard are the species beta diversity of PhyloSor and UniFrac, correlations between the phylobetadiversity indices change after integration of phylogenetic information (Table 1).

We calculated 12 phylobetadiversity indices (if weighted and unweighted abundances are included), among which five pairs were highly correlated (Figure 1, Tables 2 and 3). The highly correlated pairs were AW- D_{pw} and Rao's D , PhyloSor and UniFrac, D_{nn} and PhyloSor, D_{nn} and UniFrac, and Rao's H and P_{ST} .

Since the indices PCD and PCD_p account for the covariance of phylogenetic distance between species, we compared them with UniFrac and Π_{ST} , which also take the covariance of phylogenetic distance between species into consideration (Table 3 for the spatial scale of 100 m \times 100 m, and see Tables S2 and S3 for all other spatial scales).

2.2 Effect of abundance-weighting on phylobetadiversity

We conducted Spearman correlation analysis on three pairs of indices that differed in being either abundance-weighted or not at 4 spatial scales, namely 10 m \times 10 m, 20 m \times 20 m, 40 m \times 40 m, and 100 m \times 100 m. The difference between each pair of indices was relatively small and became larger with increased spatial scale (Figure 2). This could be explained by the change of species evenness with increased scale. Sampling of species abundance distribution at different scales supported this hypothesis (Figure 3).

Table 1 Spearman rank correlation coefficients between UniFrac and PhyloSor, UniFrac and Jaccard and PhyloSor and Sørensen at three spatial scales

Indices	20 m \times 20 m	40 m \times 40 m	100 m \times 100 m
UniFrac and PhyloSor	-1	-1	-1
UniFrac and Jaccard	0.81	0.82	0.81
PhyloSor and Sørensen	0.81	0.82	0.81

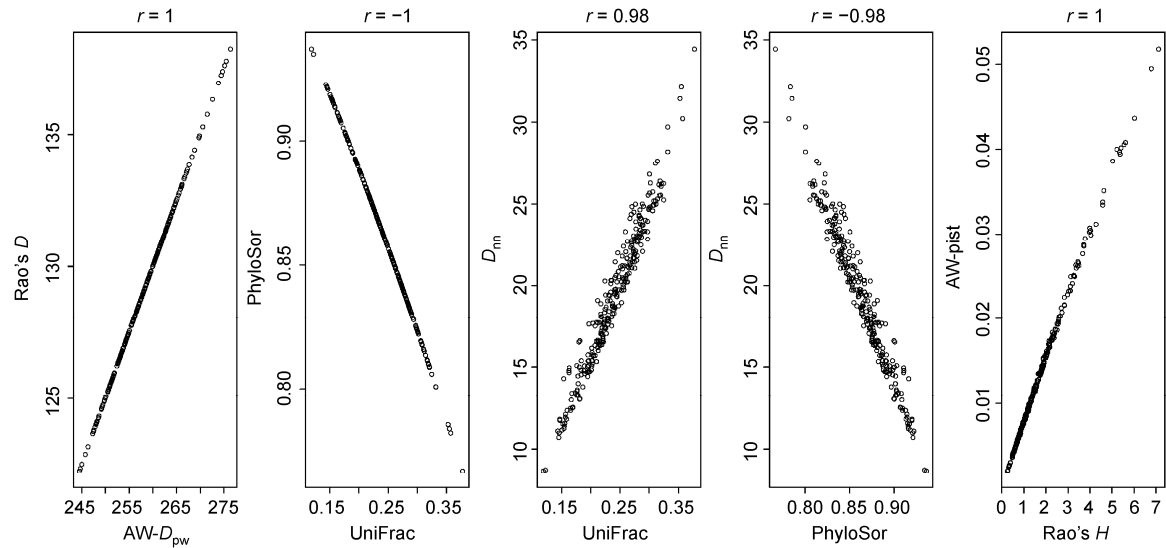


Figure 1 Spearman rank correlation coefficients between phylobetadiversity indices at a spatial scale of 100 m × 100 m.

Table 2 Spearman rank correlation coefficients between phylobetadiversity indices at a spatial scale of 100 m × 100 m; high correlation coefficients were bolded.

0.26	0.47	0.34	0.31	−0.32	0.32	1	0.47	0.41	P_{ST}
0.04	0.36	0.6	0.6	−0.55	0.55	0.42	0.36	Π_{ST}	
−0.05	1	0.11	0.17	−0.11	0.11	0.49	Rao's D		
0.25	0.49	0.34	0.32	−0.32	0.32	Rao's H			
−0.08	0.11	0.98	0.66	−1	UniFrac				
0.08	−0.11	−0.98	−0.66	PhyloSor					
−0.02	0.17	0.66	AW- D_{nn}						
−0.01	0.11	D_{nn}							
−0.05	AW- D_{pw}								
D_{pw}									

Table 3 Spearman rank correlation coefficients between phylobetadiversity indices at a spatial scale of 100 m × 100 m

0.27	0.57	0.24	Π_{ST}
0.86	0.43	UniFrac	
0.53	PCD _p		
PCD			

2.3 Ability of indices to reflect variation in community composition along habitat and spatial gradients

To find which index can best reflect the variation of phylobetadiversity along habitat and spatial gradients, we used a Partial Mantel test to partition phylobetadiversity with respect to habitat and/or spatial gradients (Table 4 for 100 m × 100 m spatial scale, and see Tables S4 and S5 for all other scales).

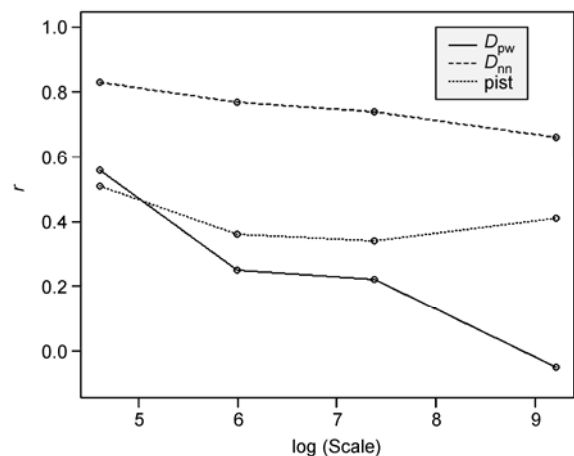


Figure 2 Effect of spatial scale on correlation coefficients between abundance-weighted and non-weighted phylobetadiversity indices.

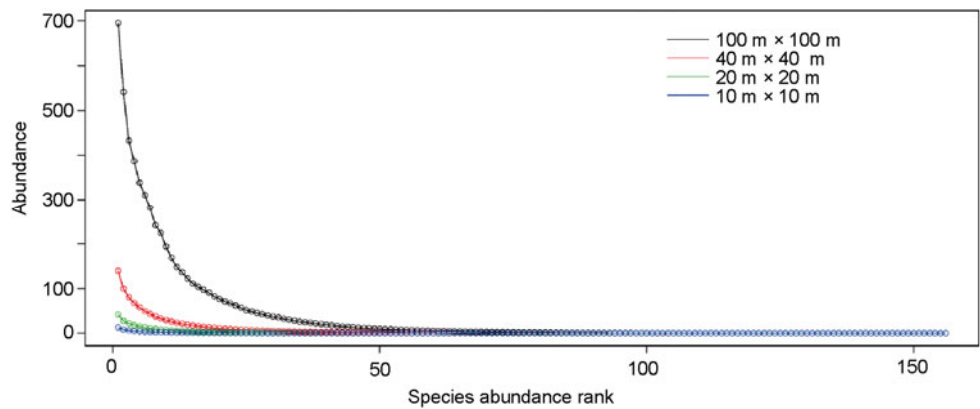


Figure 3 Absolute abundances of abundance rankings at different spatial scales.

Table 4 Results of a variation partitioning between phylobetadiversity values and habitat and spatial gradients at the spatial scale of 100 m × 100 m

Index	$a + b + c$	$a + b$	$b + c$	a	c
D_{pw}	0.025	−0.004	0.022	0.003	0.029
$AW-D_{pw}$	0.065	0.002	0.067	−0.002	0.063
D_{nn}	0.225	0.097	0.206	0.018	0.128
$AW-D_{nn}$	0.303	0.106	0.29	0.013	0.197
UniFrac	0.233	0.091	0.219	0.014	0.142
PhyloSor	0.236	0.091	0.222	0.014	0.145
Rao’s D	0.065	0.002	0.067	−0.002	0.063
Rao’s H	0.321	0.053	0.323	−0.002	0.268
Π_{ST}	0.216	0.121	0.18	0.037	0.096
P_{ST}	0.328	0.056	0.33	−0.002	0.272
PCD	0.018	0.021	0.005	0.013	−0.002
PCD_p	0.002	0.001	−0.003	0.005	0

3 Discussion

Based on species beta diversity, phylobetadiversity can provide new insights into species coexistence from phylogenetic relationships among species [6]. Niche conservation during evolutionary history plays a critical role in determining species distribution and offers a basis for phylobetadiversity studies [30,31]. Phylobetadiversity can be used to explore mechanisms of biodiversity maintenance and may have a higher utility than species beta diversity as a conservation criterion for management decisions.

3.1 Correlations between indices

Correlation analysis of phylobetadiversity indices can help us to understand better the ecological meaning of phylobetadiversity and avoid confusion. Both $AW-D_{pw}$ and Rao’s D represent abundance-weighted mean pairwise phylogenetic distance and results of the two indices are identical, so we can choose one of these indices in future studies; PhyloSor and UniFrac are derived from the Sørensen and

Jaccard indices and have similar ecological meanings, i.e., the proportion of branch length shared between species to total branch length of all species in two communities. The only difference between the two indices is that PhyloSor is an index of similarity, whereas UniFrac is an index of dissimilarity. Rao’s H and P_{ST} also have similar ecological meanings and are highly correlated; what needs further study is the finding that correlations between D_{nn} and PhyloSor, D_{nn} and UniFrac are also highly correlated. D_{nn} represents the mean nearest phylogenetic distance between two communities, whereas PhyloSor and UniFrac are the proportion of branch length between species shared relative to total branch length of all species in two communities. All of these indices represent the difference between the terminals of phylogenetic trees of species from two different communities, which may explain their strong correlation.

3.2 Effect of abundance-weighting on indices

Abundance, which reflects differences in species evenness between communities, is an important concept in community ecology. Lozupone et al. [32] found that abundance-weighted indices are suitable in studies that investigate changes in species abundance when the mechanisms may be correlated with subtle environmental changes. On the other hand, abundance-unweighted indices are used mainly to discuss factors limiting species presence.

The correlation analysis of the three pairs of indices at four spatial scales showed a decrease in strength of correlation with increasing spatial scales. In other words, when the scale is small, effect of abundance is not significant and the effect becomes more obvious as scale increases. Thus if the scale applied in an investigation is relatively small, both of each of the pairs might not need to be calculated.

3.3 Performance of indices that reflect habitat and spatial gradients

It has been shown widely that similarities between commu-

nities decrease as spatial distances between the communities increase [33]. There are two main mechanisms that explain this phenomenon: (1) habitat characteristics change with increased separation distance, and affect community composition and can be interpreted by the niche hypothesis [34]; and (2) according to neutral theory [35], although the habitat between communities may be similar, similarity between communities will decrease with increased spatial distance because of the limiting dispersal abilities of organisms.

Phylobetadiversity, as the measurement of phylogenetic distance between communities, should also decay with distance. Results of variance partitioning of phylobetadiversity between habitat and spatial distance indicate that P_{ST} and Rao's H can best reflect distance decay along habitat and spatial gradients in subtropical forest communities at the spatial scale of 100 m \times 100 m. At this scale, habitat in conjunction with spatial distance explained 32.77% and 32.1% of the variance of Rao's H and P_{ST} , respectively; however, as the spatial scale decreased to 20 m \times 20 m and 40 m \times 40 m, distance decay along spatial and habitat gradients was best reflected by $AW-D_{nn}$ and D_{nn} . At a scale of 20 m \times 20 m the variance of $AW-D_{nn}$ and D_{nn} explained by habitat factors and spatial distance was 13.4% and 9.375%, respectively, and at the 40 m \times 40 m scale 18.63% and 13.47% were explained by the same variables, respectively. Therefore we recommend using P_{ST} and Rao's H when the scales are relatively large, and $AW-D_{nn}$ and D_{nn} when scales are smaller, for studies on effects of different factors on phylobetadiversity.

We found that $AW-D_{pw}$ and Rao's D , PhyloSor and UniFrac, D_{nn} and PhyloSor, D_{nn} and UniFrac, Rao's H and P_{ST} are strongly correlated. D_{pw} , $AW-D_{pw}$, Rao's D , Rao's H , P_{ST} and Π_{ST} are based on the mean pairwise phylogenetic distance, which reflects branch differences close to the phylogenetic tree root between communities and can more effectively reflect the habitat difference than other indices. Calculations of D_{nn} , $AW-D_{nn}$, UniFrac and PhyloSor are measures of differences in phylogenetic tree terminals, which are differences in evolutionary distinctiveness [36] and may be used to reflect differences in resource utilization strategies. For these indices, abundance-weighting at small scales has little effect, but the effect of abundance increases at larger scales. At large spatial scales, habitat and space explain P_{ST} and Rao's H best, but at smaller spatial scales $AW-D_{nn}$ and D_{nn} are better explained by habitat and space.

Phylobetadiversity provides a new perspective on relationships between communities; therefore, studies combining species beta diversity and phylobetadiversity may be more comprehensive. This study analyzed correlations among phylobetadiversity indices, effects of abundance-weighting on phylobetadiversity indices at different spatial scales, and the potential of the indices to reflect spatial and habitat gradients. The findings might be helpful to researchers interested in phylogenetic ecology.

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- Whittaker R H. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monogr*, 1960, 30: 280–338
- Cody M L. Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. In: Cody M L, Diamond J M, eds. *Ecol Evolcomm*. Harvard: Harvard University Press, 1975, 214–257
- Koleff P, Gaston K J, Lennon J J. Measuring beta diversity for presence-absence data. *J Anim Ecol*, 2003, 72: 367–382
- Chen S B, Ouyang Z Y, Xu W H, et al. The research progress of beta diversity (in Chinese). *Biodiver Sci*, 2010, 18: 323–335
- Webb C O. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *Am Nat*, 2000, 156: 145–155
- Graham C H, Fine P V A. Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecol Lett*, 2008, 11: 1265–1277
- Chave J, Chust G, Thébaud C. The importance of phylogenetic structure in biodiversity studies. In: Storch D, Marquet, Brown J H, eds. *Scaling Biodiversity*, Institute Editions, Santa Fe, 2007. 151–167
- Hardy O J, Senterre B. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. *J Anim Ecol*, 2007, 95: 493–506
- Webb C O, Ackerly D D, Kembel S W. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 2008, 24: 2098–2100
- Bryant J A, Lamanna C, Morlon H, et al. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *Proc Natl Acad Sci USA*, 2008, 105: 11505–11511
- Ives A R, Helmus M R. Phylogenetic metrics of community similarity. *Am Nat*, 2010, 176: E128–E142
- Pierre L, Mi X C, Ren H B, et al. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, 2009, 90: 663–674
- Lou L H, Jin S H. Spermatophyta flora of Gutianshan Nature Reserve in Zhejiang (in Chinese). *J Beijing Forest Univ*, 2000, 22: 33–39
- Chen B, Mi X C, Fang T, et al. Gutianshan Forest Dynamic Plot: Tree Species And Their Distribution Patterns (in Chinese). Beijing: China Forestry Publishing House, 2009
- Kress W J, Erickson D L, Jones F A, et al. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proc Natl Acad Sci USA*, 2009, 106: 18621–18626
- Doyle J J, Doyle J L. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem Bull*, 1987, 19: 11–15
- Khanuja S P S, Shasany A K, Darokar M P, et al. Rapid isolation of DNA from dry and fresh samples of plants producing large amounts of secondary metabolites and essential oils. *Plant Mol Biol Rep*, 1999, 17: 1–7
- Edgar R C. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res*, 2004, 32: 1792–1797
- Zhang J L, Mi X C, Pei N C. Phylotools: Phylogenetic tools for ecologists. R package version 0.0.7.4. 201019
- Alexandros S. RAXML-VI-HP: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 2006, 22: 2688–2690
- Sanderson MJ. r8s: Inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics*, 2003, 19: 301–302
- Lemey P, Rambaut A, Drummond A J, et al. Bayesian Phylogeography finds its roots. *PLoS Comput Biol*, 2009, 9: e1000520
- Zhang L W, Mi X C, Shao H B, et al. Strong plant-soil associations

- in a heterogeneous subtropical broad-leaved forest. *Plant Soil*, 2011, doi: 10.1007/s11104-001-0839-2
- 24 Swenson N G, Anglada-Cordero P, Barone J A. Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. *Proc R Soc London Ser B*, 2011, 278: 877–884
 - 25 Ricotta C, Burrascano S. Testing for differences in beta diversity with asymmetric dissimilarities. *Ecol Indic*, 2009, 9: 719–724
 - 26 Krebs C J. *Ecological Methodology*. Menlo Park, CA: Addison-Wesley, 1999
 - 27 Lozupone C, Hamady M, Knight R. UniFrac—An online tool for comparing microbial community diversity in a phylogenetic context. *BMC Bioinformatics*, 2006, 7: 371–384
 - 28 Rao C R. Diversity and dissimilarity coefficients: A unified approach. *Theor Popul Biol*, 1982, 21: 2443
 - 29 Helmus M R, Bland T J, Williams C K, et al. Phylogenetic measures of biodiversity. *Am Nat*, 2007, 169: E68–E83
 - 30 Donoghue M J. A phylogenetic perspective on the distribution of plant diversity. *Proc Natl Acad Sci USA*, 2008, 105: 11549–11555
 - 31 Cavender-Bares J, Ackerly D D, Baum D A, et al. Phylogenetic overdispersion in Floridian oak communities. *Am Nat*, 2004, 163: 823–843
 - 32 Lozupone C A, Hamady M, Kelley S T, et al. Quantitative and qualitative beta diversity measures lead to different insights into factors that structure microbial communities. *Appl Environ Microbiol*, 2007, 73: 1576–1585
 - 33 Soininen J, McDonald R, Hillebrand H. The distance decay of similarity in ecological communities. *Ecography*, 2007, 30: 3–12
 - 34 Nekola J C, White P S. The distance decay of similarity in biogeography and ecology. *J Biogeogr*, 1999, 26: 867–878
 - 35 Hubbell S P. *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press, 2001
 - 36 Redding D W, Mooers A O. Incorporating evolutionary measures into conservation prioritization. *Conserv Biol*, 2006, 20: 1670–1678

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Supporting Information

- Table S1** Principal component analysis of environmental factors at the spatial scale of 100 m × 100 m
- Table S2** Spearman rank correlation coefficients between phylobetadiversity indices at spatial scale of 40 m × 40 m
- Table S3** Spearman rank correlation coefficients between phylobetadiversity indices at spatial scale of 20 m × 20 m
- Table S4** Results of Mantel test between phylobetadiversity values and habitat and spatial gradients at a spatial scale of 40 m × 40 m
- Table S5** Results of Mantel test between phylobetadiversity values and habitat and spatial gradients at a spatial scale of 20 m × 20 m

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