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Is Phylogeny More Useful than Functional Traits for Assessing Diversity Patterns Under Community Assembly Processes?

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Abstract: Phylogenetic and functional diversities and their relationship are important for understanding community assembly, which relates to forest sustainability. Thus, both diversities have been used in ecological studies evaluating community responses to environmental changes. However, it is unclear whether these diversity measures can uncover the actual community assembly processes. Herein, we examined their utility to assess such assembly processes by analyzing similarities in phylogenetic, functional, and taxonomic α - and β -diversities along an elevational gradient. Additionally, we examined the relationships among environment, phylogeny, and functional traits within the community. Based on our results, we evaluated whether phylogenetic or functional diversity could better reveal the actual community assembly processes. We found that taxonomic, phylogenetic, and functional α -diversities were correlated with one another. Although the functional α -diversity showed a linear correlation with the elevational gradient, taxonomic and phylogenetic α -diversities showed unimodal patterns. Both phylogenetic and functional β -diversities correlated with taxonomic β -diversity, but there was no significant relationship between the former. Overall, our results evidenced that phylogenetic diversity and taxonomic diversity showed similar patterns, whereas functional diversity showed a relatively independent pattern, which may be due to limitations in the functional trait dimensions used in the present study. Although it is difficult to unravel whether the environment shapes phylogeny or functional traits within a community, phylogenetic diversity is a good proxy for assessing the assembly processes, whereas functional diversity may improve knowledge on the community by maximizing information about the functional trait dimensions.

Keywords: community assembly; phylogenetic diversity; functional trait; taxonomic diversity

1. Introduction

Documenting and exploring the patterns of taxonomic, phylogenetic, and functional diversities have been lead themes in ecology [1]. The Shannon-Wiener index, a widely used taxonomic diversity metric, combines species richness and abundance to describe species interactions and ecological processes heuristically within/among communities [2]. However, it is difficult to assess community assembly patterns from taxonomic data, because species presence/absence data are a limitation for the analysis of the abundance-weighted null model. Therefore, although taxonomic diversity is a



direct result of the community assembly processes, researchers should resort to using indirect data (i.e., phylogenetic or functional traits) as alternative measures to overcome the limitation imposed by species presence/absence data on the direct estimation of community assembly processes [1]. Phylogenetic diversity is used to compare relatedness among species within a community [2–4], while functional diversity is used to assess aspects of diversity in relation to the traits that affect ecosystem function [5,6]. Accordingly, diversity metrics based on phylogenetic relatedness or functional traits have been used as proxies to explain species composition within a community or species turnover among communities [7–9]. Nevertheless, both phylogenetic and functional diversities are associated with community assembly processes [8,10–12] and ecosystem stability [13].

In general, phylogenetic diversity can be used as a proxy for quantifying functional diversity [11] when functional traits are difficult to obtain, as closer phylogenetic relationships may indicate phylogenetically conserved traits [14]. However, some variable traits, such as leaf morphology, may not be replaced by phylogeny. Moreover, phylogenetic diversity may be used to elucidate species similarities and differences (i.e., taxonomic diversity) [15–17], while functional diversity may indicate how species are distributed in the multidimensional space [18,19]. When compared, taxonomic, functional, and phylogenetic diversities have the potential to reveal the assembly of species communities [15,20]. Thus, considering the phylogenetic and functional components of diversity may help elucidate community assembly processes that can explain patterns in species diversity and distribution at a community level [1,6,8,21,22]. However, few studies have combined taxonomic, phylogenetic, and functional diversities [8,23,24].

Previous studies have explored one of these diversity metrics [15,25,26], along soil nutrient [27,28], disturbance [8,29], and elevational [4,8] gradients in tropical rain forests (e.g., [21]), temperate forests (e.g., [30,31]), and grasslands [32]. However, the correlations between these diversities are still unclear, and thus these metrics have not been used to explore community–environment relationships. In the present study, we used taxonomic, phylogenetic, and functional diversities along an elevational gradient in Mount Taibai (China), which is the highest mountain in mid-eastern China, to assess their performance under changing environmental conditions. In this area, elevation seems to be the most important gradient, as there are substantial environmental changes in a relatively short geographic range [33], because elevation may drive considerable changes in abiotic factors, such as water availability, temperature, and soil properties [34]. Therefore, we explored the relationships between taxonomic, phylogenetic, and functional diversities display a similar or consistent pattern along the elevational gradient, and (ii) whether phylogenetic data is a proxy of functional traits. The results of the present study contribute to improving the understanding of the relationships between species composition, phylogeny, and functional traits within a community.

2. Materials and Methods

2.1. Study Site

The study was carried out in Mount Taibai (33°40′–34°10′ N, 107°19′–107°50′ E), the highest peak in the Qinling Mountains, China. The highest elevation in this region is 3767.2 m. A natural reserve encompassing the zone surrounding Mount Taibai was established in 1965, and since then, no significant forest fire or human disturbance has been recorded in the area [33]. The mean annual temperature of Mount Taibai is 0.9–12.3 °C [35]. Annual precipitation is 640–1000 mm, with a humped pattern of rainfall distribution along the elevational gradient. Plant diversity is high in this area, with 389 woody plant species [36], distributed along the elevational gradient of Mount Taibai [33]. For the present study, we selected the core forest area, with an elevation 1140–3481 m. Such a wide range provided the unique opportunity to explore diversity shifts along the elevational gradient with abrupt changes in environmental conditions.

2.2. Establishment and Sampling of Plots

Thirty-nine plots (20×30 m) were randomly established along the elevational gradient. Information on each plot latitude, longitude, and elevation (Figure 1) was recorded using a Global Positioning System (GPS; HOLUX EZ-Tour; HOLUX Technology Inc., Hsinchu, Taiwan). Within each plot, all woody plants with a diameter at breast height (DBH) >8 cm were identified to the species level, and their height and abundance were recorded. Whenever possible, we collected 20 leaves from twigs pointing in every direction, from at least five individuals of each species within each plot. The leaves were wrapped in wet filter paper and transported to the laboratory.



Figure 1. Location of the sampling plots in Mount Taibai. The curves represent contour lines and the numbers refer to elevation (m). The solid squares indicate the location of each plot.

2.3. Measurement of Functional Traits

The analysis of the functional traits should include traits belonging to at least four dimensions [37], including the so-called "intrinsic dimension" [38]. To maximize the intrinsic dimensionality of the plant functional traits, we selected the maximum plant height as the morphological character; leaf area (LA), specific leaf area (SLA; which responds to drought/water availability), and leaf dry matter content (LDMC; which responds to temperature) as the spectral characters [39]; leaf nitrogen content (LNC) and leaf carbon content (LCC) as the chemometrical characters [40,41]; and seed mass (SM) as the reproductive character. The leaves collected from the study plots were used to measure the LA, SLA, LDMC, LNC, and LCC. After scanning the leaves, the LA was calculated using ImagePro Plus 6.0 (MEDIA CYBERNETICS Inc., Rockville, MD, USA). The SLA and LDMC were measured following standard methods [42], and the LNC and LCC were measured using an elemental analyzer (EA3000, EuroVector Inc., Pavia, Italy) and standard methods [42]. The SM data were obtained from a database on seed weight resulting from a previous study [34]. We also weighed some seeds preserved at the

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specimen museum in Xi'an Botany Garden, Shaanxi, China. The missing SM data were complemented using data published for the flora of the Qinling Mountains and from the Kew Seed Information Database (http://data.kew.org/sid/sidsearch.html).

2.4. Phylogenetic Analysis

The size of the potential regional species pool (i.e., the 389 woody species identified in Mount Taibai [43]) was suitable for constructing a supertree for the phylogenetic analysis [44]. The evolutionary branch length of each species was inserted using Phylomatic (www.phylomatic.net), and Phylocom 3.0 (designed by Webb, Ackerly & Kembel) [45] was then used to construct the supertree based on the phylogenetic data and evolutionary branch length of each species [11].

2.5. Data Analyses

The Shannon-Wiener index was calculated using Biotools software (based on Excel 2003) based on species abundance data, and then used as the taxonomic α -diversity index. In addition, the species richness was calculated for each plot, as this is another useful index to describe the level of α -diversity [21]. As the analysis of β -diversity usually involves species turnover between pairs of samples [46], we calculated the Jaccard index as taxonomic β -diversity matrices of plot pairs using the "vegan" package of R 3.6.1 (https://www.r-project.org/). Faith's phylogenetic diversity [17] was calculated by using Phylocom 3.0 and the "PD" package in R 3.6.1. These indices were used to measure the phylogenetic α -diversity. The phylogenetic β -diversity (β NTI) of the plot pairs was also calculated using Phylocom 3.0(designed by Webb, Ackerly & Kembel), by its "COMDIST" model. The algorithm of β NTI [47], is as follows:

$$\beta NTI = -1 \times \frac{\beta MNTD_{observed} - \beta MNTD_{randomized}}{sd \ \beta MNTD_{randomized}}$$
(1)

MNTD represents the mean nearest phylogenetic taxon distance, *observed* means observed value, *randomized* means randomized value, β means the differentiation between two plots, and *sd* means standard deviation. Before we calculated the functional diversity, we calculated the community-weighted mean functional traits (CWM) by the functional traits and relative abundance of each species [48], because abundance-weighted, community-level measures of functional diversity are better predictors of ecosystem processes than those based on un-weighted metrics [49,50]. We calculated Mason's functional α -diversity (F_{α}) [51] based on all of the functional traits, measured and Mason's functional β -diversity (F_{β}) [52] based on the comprehensive trait data. The functional diversity was calculated using the "FD" package in R 3.6.1. The algorithms of F_{α} and F_{β} , are as follows:

$$F\alpha = \sum Pi(xi - \overline{x}) \tag{2}$$

$$F\beta = \sum \frac{1}{n} (\bar{x}k - \bar{x}region)$$
(3)

 P_i is the relative abundance of species *i*, x_i is the functional trait value of species *i*, \overline{x} is the mean functional trait value of all species, \overline{x}_k is the CWM of community *k*, and \overline{x}_{region} is the mean functional trait value of the whole study region.

Regression fitting was used to explore the relationships between the diversities and the elevational gradient. We performed linear fitting when the relationship was significant and non-liner fitting when it was not. To avoid pseudoreplication due to the increased number of observations of β -diversity, the multiple regressions on distance matrices (MRM), which can be used to relate the phylogenetic or functional β -diversity to the spatial and elevational distance [53–55] was applied before the regression analysis. MRM was run by "ecodist" package in R 3.6.1. If there was a significant correlation between the variations in elevation (Δ Elevation) and β -diversity, a regression analysis was used. Regression graphs were drawn using Origin 8.0 (OriginLab Co., Studio City, CA, USA). In addition, we explored

the relationships between taxonomic, phylogenetic, and functional diversities using correlation analysis; Pearson's correlation coefficients and one-way analysis of variance (ANOVA) were calculated in SPSS 19.0 (IBM, Armonk, NY, USA).

3. Results

3.1. α -Diversity

In this study, 142 woody species were recorded. For each plot, there were 15.56 species on average. The Shannon-Wiener and species richness indices showed similar trends with increasing elevation (Figure 2). The trend in phylogenetic α -diversity (Faith's PD) along the elevational gradient was similar to that of taxonomic α -diversity, with its maximum value at 2000 m (the maximum values of Shannon-Wiener and species richness indices were also recorded at approximately 2000 m; Figure 2). However, the functional α -diversity showed a different pattern from that of the taxonomic and phylogenetic α -diversities. It displayed a tendency to decrease monotonically along the elevational gradient (FD in Figure 2).



Figure 2. α -diversity along the elevational gradient. Shannon-Wiener (A) and species richness (B) indices describe taxonomic α -diversity, while PD (phylogenetic α -diversity; Faith's PD, C) and FD (F_{α} , D) describe the phylogenetic and functional α -diversities, respectively. The line in each graph corresponds to the significant fitting line (p < 0.05).

3.2. β -Diversity

 β -diversity describes the differences in terms of turnover and nestedness between the species composition of each plot pair when the elevation is different (i.e., with Δ Elevation) between the two plots. The MRM showed that elevation was the key factor affecting β -diversity (21.2% interpret ability for taxonomic, 15.51% interpret ability for phylogenetic, and 19.82% interpret ability for functional

β-diversity; elevation has the highest interpretability for each β-diversity). Also, there were significant correlations between Δ Elevation and the three β-diversities (p = 0.001 for taxonomic, p = 0.01 for phylogenetic, and p = 0.002 for functional β-diversity). The taxonomic β-diversity (Jaccard index) tended to increase gradually with Δ Elevation. Relatively small differences in elevation corresponded to sharp increases in taxonomic β-diversity. However, when Δ Elevation reached approximately 500 m, the increase in taxonomic β-diversity was less evident. The phylogenetic and functional β-diversities showed a weak linear increase with Δ Elevation compared with that of taxonomic β-diversity (Figure 3).



Figure 3. Taxonomic (Jaccard, A), phylogenetic (β NTI, B), and functional (F_β , C) β -diversities along the Δ Elevation gradient. Species β -diversity refers to taxonomic β -diversity. Δ Elevation means the elevational difference between each plot pair. The gray line in each graph represents the significant fitting line (p < 0.05).

3.3. Relationships between Taxonomic, Phylogenetic, and Functional Diversities

Pearson's correlation coefficients for the relationships between the α -diversity indices are shown in Table 1. Although there were significant positive correlations between the indices, phylogenetic diversity showed higher correlations with taxonomic α -diversity indices, particularly with species richness, than functional diversity, which showed lower correlations to the taxonomic α -diversity indices than phylogenetic diversity. Pearson's correlation coefficients for the β -diversity indices are shown in Table 2. The phylogenetic β -diversity showed a significant positive correlation with taxonomic β -diversity, whereas functional β -diversity showed a relatively weak correlation with taxonomic β -diversity. However, there was no correlation between phylogenetic and functional β -diversities (Table 2).

	Shannon-Wiener	Species Richness	Phylogenetic Diversity
Species richness	0.839 **		
Phylogenetic diversity	0.779 **	0.933 **	
Functional diversity	0.620 **	0.471 **	0.571 **

Table 2. Pearson's correlation coefficients between taxonomic, phylogenetic, and functional β -diversities. * indicates significance at p < 0.05. ** indicates significance at p < 0.01.

	Phylogenetic Diversity	Functional Diversity
Functional diversity	-0.050	
Taxonomic diversity	0.289 **	0.196 *

4. Discussion

Our results showed that the taxonomic, phylogenetic, and functional α -diversities were correlated along the elevational gradient. These results were similar to those of previous studies, in which the functional and phylogenetic diversities were positively correlated with the taxonomic diversity [13, 24,56,57]. However, in the present study, the three α -diversity metrics showed a consistent decline in the high elevation region (Figure 2), suggesting that severe conditions may lead to decreasing biodiversity [58] due to environmental filtering [6,59]. This decrease in species richness may then lead to decreasing phylogenetic and functional diversities.

Generally, four patterns can be described for the relationship between α -diversity and elevation, namely: humped, decreasing, increasing, and no discernible trend [60]. For instance, a considerable, mostly linear decrease in diversity with increasing elevation has been found at mid-altitudes in the tropical Andes [61]. In addition, diversity at low altitudes is higher than diversity at mid- to high-altitudes [62]. In the present study, both taxonomic (including Shannon–Wiener and species richness indices) and phylogenetic α -diversities showed unimodal patterns along the elevational gradient, mostly caused by environmental filtering at the highest (low temperature) and lowest (human disturbance) altitudes [33], whereas functional α -diversity showed a monotonically decreasing pattern. This difference between taxonomic/phylogenetic diversities and functional diversity suggests that the latter, based on a limited number of traits, may not fully reveal the taxonomic changes within a community along a gradient, as functional α -diversity correlates only partially with phylogenetic α -diversity [11,63]. It is important to note that we used Faith's phylogenetic diversity, which is richness relevant and non-abundance weighted. Because of the algorithm of the phylogenetic structure (net relatedness index (NRI) or nearest taxon index (NTI)), a non-abundance-weighted metric is suitable. However, based on the algorithm of the functional structure (Standardised Effect Sizes, SES-metric), an abundance-weighted metric is needed, as supported by our results for β -diversity. A 500-m variation in elevation corresponded to a plateau in taxonomic β -diversity. This is mostly due to environmental heterogeneity, as the distance between two plots was short enough not to lead to dispersal limitation [33]. Although both phylogenetic and functional β -diversities were correlated to taxonomic β -diversity to some extent (Figure 3 and Table 2), the phylogenetic and functional β -diversities were unrelated (Table 2), as previously reported [64]. Thus, although species/phylogenetic turnover can occur, functional traits may not turnover [12]. Based on the present results, we may also conclude that phylogenetic and functional diversities show relatively weak responses to environmental changes, especially β -diversities. However, it is difficult to state that the environment shapes phylogenetic and functional diversities independently. Some researchers have claimed that phylogenetic and functional diversities may be closely related to each other owing to evolutionary conservatism [16], and that they may also be similar to taxonomic diversity [8]. We calculated functional diversity using a

comprehensive set of data involving several traits in multiple dimensions, but this might not have been sufficient for capturing the intrinsic dimension and fully describing the functional variation of the species comprised in our study [38]. Therefore, more functional trait dimensions may be needed in order to assess the relationship between the phylogenetic and functional diversities along a gradient.

As the phylogenetic diversity showed a similar pattern to both taxonomic α - and β -diversities, we recommend the use of phylogenetic diversity as the proxy to assess the assembly processes, especially when the intrinsic dimensionality of the functional traits is lacking. In fact, one functional trait may represent only one aspect of response of the community along resource availability [11,65]. Thus, it is necessary to explore continuous measures of functional diversity based on a variety of traits to increase our understanding of assembly processes [66]. On the contrary, phylogenetic diversity may be a useful measure to consider taxonomic changes that are linked to niche differentiation, resource partitioning, and other ecological processes [67–69]. Similarly, Meynard et al. [8] suggested that environmental change may lead to some shifts in the community's phylogeny. In addition, phylogeny may reflect the accumulated evolutionary history of a community, which is related to the assembly processes, and therefore it would be related to either the system's capacity to generate new evolutionary solutions in the face of change or to persist despite those changes [8], and it provides additional value for theoretical ecology [70]. In other words, phylogenetic diversity may reveal a more accurate picture of theassembly processes than functional diversity, unless the latter contains enough trait dimensions.

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