

Research Article

A taxonomic and phylogenetic perspective on plant community assembly along an elevational gradient in subtropical forests

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Abstract

Aims Biodiversity patterns along elevational gradients have been well documented. Yet, the variations of biodiversity patterns along elevations and their underlying mechanisms are still unclear. Integrating multiple facets of biodiversity provides novel insights into the mechanisms for driving community assembly. In this study, species abundance information was incorporated into taxonomic and phylogenetic diversity to reveal the ecological and evolutionary forces of plant community assembly along an elevational gradient in subtropical forests.

Methods We selected 17 woody plant plots along an elevational gradient from 270 to 1470 m in eastern China's subtropical forests. Both presence-based and abundance-based measures of angiosperm species were used to quantify taxonomic alpha diversity, phylogenetic alpha diversity, phylogenetic relatedness, as well as taxonomic and phylogenetic dissimilarity among these plots. And the relations between these measures and climatic and topographic variables were analyzed.

Important Findings For both abundance-weighted and unweighted measures, we observed an overall increasing pattern for taxonomic alpha diversity along elevation, and distance-decay trends of taxonomic and phylogenetic similarity with increased elevational distances. However, there were disparity patterns of phylogenetic alpha diversity between abundance-weighted and unweighted measures. For phylogenetic structure, there was no significant trend along elevation. Both topographical and microclimatic variables were main drivers of diversity patterns and phylogenetic structure. Compared with unweighted measures, abundance-weighted measures were strongly related with the slope and stand basal area. Overall, our results prove that deterministic processes mediated by local species abundance imprint on plant community composition along the elevational gradient.

Keywords community phylogenetics, phylogenetic structure, phylogenetic diversity, beta diversity, environmental gradient, microclimate, phylogenetic niche conservatism

亚热带森林植物群落沿海拔梯度的分类与系统发育研究

摘要: 生物多样性沿海拔梯度的分布格局已受到广泛关注。然而,生物多样性格局沿海拔梯度的变异及其潜在机制尚不清楚。整合生物多样性的多维度信息为理解群落构建机制提供了新思路。本研究在我国东部亚热带森林沿海拔270–1470 m的梯度上设置了17个木本植物固定样地,分析了沿海拔梯度植物群落构建的生态和进化驱动力。基于样地内物种出现(0–1数据)和多度信息,计算群落内被子植物的物种和系统发育alpha和beta多样性、系统发育结构等,并量化多样性指标与微气候和地形之间的关系。研究发现,不论多度加权与否,物种alpha多样性均沿海拔升高而增加,物种和系统发育的相似性随海拔距离的增加而呈衰减趋势。然而,多度加权与否会形成不同的系统发育alpha多样性格局。对于系统发育结构而言,沿海拔增加并无明显趋势。地形和微气候是多样性格局和系统发育结构的主要驱动力。与未考虑物种多度的多样性指标相比,多度加权的指标与坡度和胸高断面面积相关性更高。这些结果表明,由局域物种多度介导的确定性过程对沿海拔梯度的植物群落构建具有一定影响。

关键词: 群落系统发育, 系统发育结构, 系统发育多样性, beta多样性, 环境梯度, 微气候, 系统发育生态位保守性

INTRODUCTION

Understanding how biodiversity varies ecologically and evolutionarily across geographic gradients like latitudinal or elevational gradients is one of the fundamental questions in biogeography and macroecology (Lomolino *et al.* 2017; Sanders and Rahbek 2012). Elevational gradients have long been realized and served as natural experiments to study biodiversity patterns and the underlying mechanisms (Lomolino 2001; McCain and Grytnes 2010; Rahbek *et al.* 2019b; von Humboldt 1849). Compared with latitudinal gradients, elevational gradients have much steeper environmental gradients within a short geographical distance and represent a large variety of ecosystems along elevations, ranging from tropical forests at the bottoms to alpine tundra at the peaks in some mountains (Roy and Behera 2005). Ever since the pioneering work in Mt. Chimborazo by Alexander von Humboldt over 200 years ago (von Humboldt 1849), a lot of studies have been done to document biodiversity patterns and the underlying drivers along elevations (McCain and Grytnes 2010; Rahbek 1995). On the one hand, biodiversity along elevations vary dramatically across taxa and regions, showing either monotonically decreasing, hump-shaped or monotonically increasing patterns (Bryant *et al.* 2008; Guo *et al.* 2013; Rahbek 2005). On the other hand, it remains unclear that how evolutionary and ecological processes shape species distributions and biodiversity in mountains (Rahbek *et al.* 2019a). Therefore, building a strong connection between the observed patterns of biodiversity and these key

evolutionary and ecological processes is critical for a fundamental understanding of mountain biodiversity (Rahbek *et al.* 2019a; Vellend 2016).

Contemporary species diversity and species' distributions are attributed to the interactions between species and their environments and the long-term evolution of species (Lomolino *et al.* 2017). However, previous studies commonly used species-centered methods such as species richness, treating all species as ecologically equivalent and ignore the evolutionary difference among species (Webb *et al.* 2002). Along with the rapid development in molecular phylogenetics, phylogenetic relatedness is used as a proxy for ecological differences among species. It is combined with taxonomic diversity to explain biodiversity patterns along elevations (e.g. Culmsee and Leuschner 2013; He *et al.* 2017; Kandlikar *et al.* 2018; Smith *et al.* 2014), but no general pattern of taxonomic and phylogenetic diversity has been documented. For example, both taxonomic and phylogenetic richness along elevations decreased in northeastern China (Qian *et al.* 2014) and northern Ecuador (Worthy *et al.* 2019), while contrasting patterns of taxonomic and phylogenetic richness were documented in Malesia (Culmsee and Leuschner 2013), South Korea (Chun and Lee 2017) and Japan (Tanaka and Sato 2015). The results in taxonomic and phylogenetic beta diversity along elevations were also inconsistent. Zhang *et al.* (2016) found that both taxonomic and phylogenetic turnover increased with elevational distances in northern China. However, Kandlikar

et al. (2018) found that elevational distance in Costa Rican plant communities was strongly related with taxonomic dissimilarity, but not with phylogenetic dissimilarity.

Community phylogenetic structure along elevations has been investigated to unravel the assembly rules of plant communities. This phylogenetic approach hinges on the phylogenetic niche conservatism hypothesis that the tendency of species' niche within a lineage to be stable over evolutionary time, indicating that closely related species usually share similar habitat preferences (Losos 2008; Wiens *et al.* 2010; Wiens and Graham 2005; Willis *et al.* 2008). Environment filtering along elevational gradients is expected to lead to species within communities more closely phylogenetically related to each other (phylogenetic clustering) than expected (González-Caro *et al.* 2014; Machac *et al.* 2011; Qian *et al.* 2013). By contrast, if interspecific interactions such as competitive exclusion play a major role during community assembly, stable coexistence could be achieved through niche differentiation, under which the community structure is phylogenetic overdispersion (Slingsby and Verboom 2006; Webb *et al.* 2006). Phylogenetic clustering has been identified within high-elevation communities in Mt. Changbaishan (Qian *et al.* 2014) and Hengduan Mountains region in China (Li *et al.* 2013), European Alps in France (Marx *et al.* 2017) and Mt. Rausu in Japan (Kitagawa *et al.* 2018). However, other studies in the Rocky Mountains (Bryant *et al.* 2008), Andes (Qian 2017) and Malesia of tropical Asia (Culmsee and Leuschner 2013) have shown phylogenetic clustering at low elevations and overdispersion at high elevations. These contrasting patterns of phylogenetic structure suggested the necessity of further studies to gain insights into the underlying mechanisms of elevational biodiversity patterns.

Several reasons contribute to these inconsistent patterns of biodiversity and community phylogenetic structure along elevations. First, species abundance is critical for ecological processes and dynamics (Hillebrand *et al.* 2008) and can add new insights into species coexistence and the maintenance of biodiversity and ecosystem functions (Devictor *et al.* 2010). Along an Andean elevational gradient in Ecuador, tree species richness decreased with elevation while species evenness had no trend (Worthy *et al.* 2019). When species abundance was included, community phylogenetic structure changed from clustering to random in western Amazon

basin (Eiserhardt *et al.* 2013) and from clustering to overdispersion in eastern Australia (Sommer *et al.* 2017). Second, the microclimate where plants actually live is highly heterogeneous across space and time, and differs strongly from their surrounding macroclimate (Kearney and Porter 2009; Sears *et al.* 2011), whereas previous studies of plant–climate interactions usually use coarse-resolution climate data (e.g. WorldClim and CHELSA). Recent studies have demonstrated that fine-resolution microclimate data can help us better explore biodiversity patterns from an evolutionary and ecological perspective (Potter *et al.* 2013).

In this study, taxonomic and phylogenetic diversity and community phylogenetic structure of angiosperm plant assemblages along an elevational gradient in Chinese subtropical forests were quantified. This region covers more than 25% of the area of China, ranging from 22° to 33° N in latitude and 98° to 123° E in longitude (Song 1988; Song *et al.* 2013). The high temperature and rainy climate make the subtropical forests have complex flora and extremely high species diversity, harboring more than 14 600 vascular plant species that account for more than 40% of the species recorded in China (Lin 1982). Meanwhile, a lot of relict and endemic species occurred in this region due to the long-term relatively stable climate and complex topography (Lu *et al.* 2018; Tang *et al.* 2018). By combining the data from plant survey, phylogeny and microclimate monitoring along an elevational gradient in the eastern part of the subtropical region, the primary goals of this study are to: (i) investigate the patterns of taxonomic and phylogenetic alpha and beta diversity along the gradient; (ii) evaluate phylogenetic structure of the plant communities along the gradient; (iii) identify the key environmental variables in shaping plant diversity patterns and community assembly. This work sheds insights on the ecological and evolutionary forces that drive community assembly along environmental gradients and suggests the need for an integrative approach to biodiversity conservation.

MATERIALS AND METHODS

Study area

This study was conducted along an elevational gradient on Mt. Tianmu in the northwest of Zhejiang Province, China. A majority of the mountain is located within the Mt. Tianmu National Nature Reserve (30°18'30"–30°21'37" N,

119°24'11"–119°27'11" E), and has a total area of 42.84 km². The mountain peak is at 1506 m a.s.l. This region is mainly influenced by the Pacific monsoon climate, with mean annual temperature varying from 8.8 to 14.8 °C, and annual precipitation ranging from 1390 to 1870 mm (Jiang and Zhang 1992). Due to the steep terrain and drastically climatic variations along elevation, Mt. Tianmu has an obvious vertical distribution zone of vegetations: (i) evergreen broad-leaved forest (<950 m); (ii) evergreen and deciduous broad-leaved mix forest (950–1100 m); (iii) deciduous broad-leaved forest (>1100 m) (Da *et al.* 2009). Although this mountain has been protected from logging since the year 1956 and became the national nature reserve in 1986, it is not fully isolated from human disturbance (e.g. tourism-related activities) since it is located close to highly urbanized regions (e.g. Hangzhou city).

In 2017–2018, seventeen 20 m × 20 m plots along an elevational gradient were set up from 270 to 1470 m above the sea level in this mountain (Fig. 1). These plots belong to the BEST (Biodiversity along Elevational gradients: Shifts and Transitions) research network (<https://best-mountains.org>), which currently include over 100 permanent monitoring plots along elevations in 11 mountains. The plots were set at intervals of ~100 m in elevation, and one or two plots were set at each interval, considering the complexity of vegetation composition. Within each plot, all woody stems with ≥1 cm DBH (diameter at breast height) were tagged and identified to species. The Latin name of the species was standardized according to The Plant List v1.1 (<http://www.theplantlist.org>), the Flora of China (Wu *et al.* 1994–2013) and the Flora of Mt. Tianmu (Ding 2010). Considering the huge differences in evolutionary

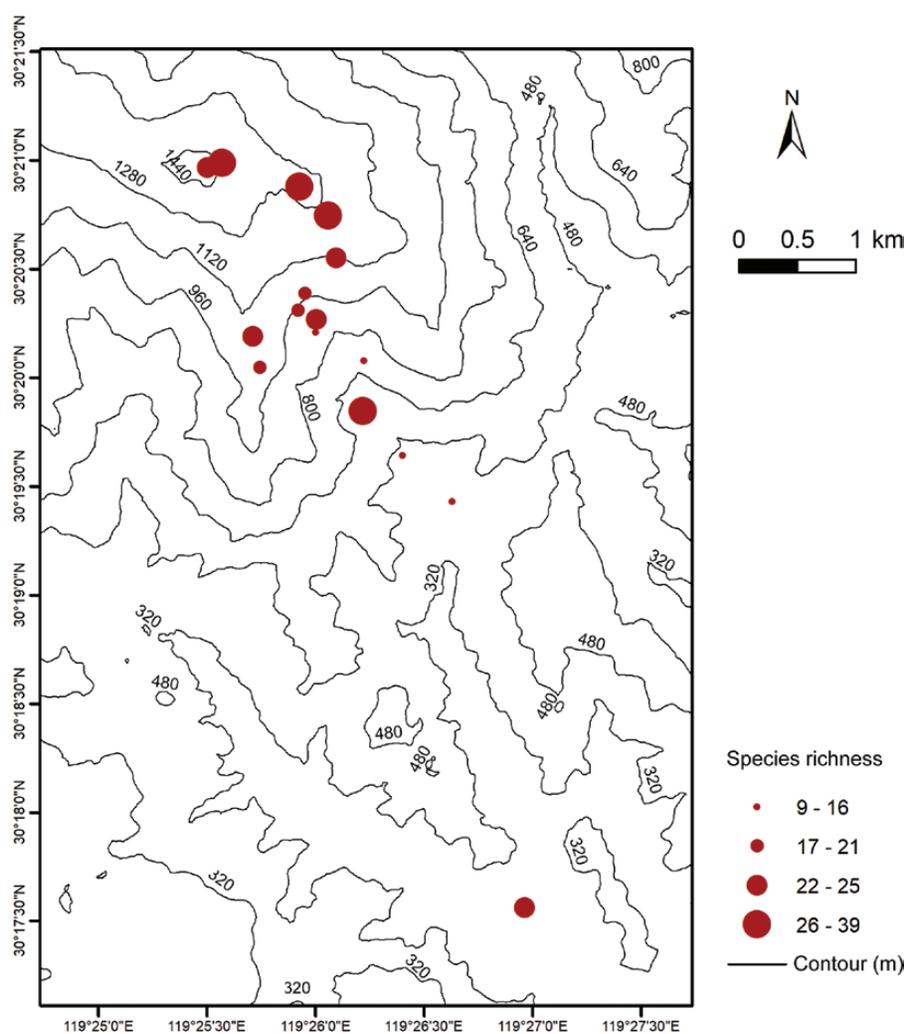


Figure 1: The location of the 17 study plots and the pattern of species richness along the elevational gradient in Mt. Tianmu, Zhejiang Province.

history between gymnosperms and angiosperms, only the angiosperms were kept for the current analysis. Overall, there were 2326 angiosperm individuals occurred within these plots, belonging to 42 families and 154 species.

Phylogeny tree construction

We used the R package *VPhyloMaker* (Jin and Qian 2019) to construct a species-level phylogenetic tree. This package contains a mega-phylogeny, which was a combination of GBOTB for seed plants (Smith and Brown 2018) and the clades in Zanne *et al.* (2014)'s phylogeny. Among the 154 species, 117 (76%) species were included in the mega-tree. For the remaining 37 species that were not found in the mega-phylogeny, we randomly added species within its respective genus using the BLADJ approach.

Metrics of community diversity and phylogenetic structure

Taxonomic and phylogenetic alpha diversity

Species richness was used to quantify taxonomic alpha diversity. We calculated the phylogenetic alpha diversity using the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD). Faith's phylogenetic diversity (Faith 1992) was excluded for the current analysis due to the strong correlation with species richness (Pearson's correlation coefficient = 0.951, $P < 0.001$). MPD calculates mean pairwise phylogenetic distance between all possible pairs of taxa within a community and can detect the overall phylogenetic divergence of species (Kembel *et al.* 2010). MNTD is the average of the phylogenetic relatedness between each taxon and its nearest relative within a community and can reflect species' recent adaptation (Kembel *et al.* 2010). To consider the effect of species abundance, we calculated the Shannon–Wiener diversity index (Shannon 1948), and abundance-weighted MPD and MNTD. The formula of abundance-weighted MPD/MNTD is as follows:

$$\text{Abundance-weighted MPD/MNTD} = \frac{\sum_i^n \sum_j^n \delta_{ij} f_i f_j}{\sum_i^n \sum_j^n f_i f_j} \quad (\text{where } i \neq j) \quad (1)$$

where $\delta_{i,j}$ is the phylogenetic distance or nearest phylogenetic distance between species i and j , f represents species relative abundance and n is the number of species in the community (Swenson 2014). These metrics of phylogenetic alpha diversity

were computed using R package *picante* (Kembel *et al.* 2010).

Taxonomic and phylogenetic beta diversity

Two measures of taxonomic beta diversity were calculated: the Jaccard index for species composition dissimilarity among the plots (Jaccard 1901) and the Bray–Curtis index for abundance-weighted taxonomic beta diversity (Chao *et al.* 2005). These indices were calculated using R package *betapart* (Baselga and Orme 2012). Phylogenetic beta diversity for both presence/absence data and abundance data were measured by using the MPD and MNTD between species pairs from two communities. These measures were calculated using R package *picante* (Kembel *et al.* 2010).

Phylogenetic structure of plant community

To measure the degree of phylogenetic relatedness among co-occurring species within each community, the nearest taxon index (NTI) and net relatedness index (NRI) were used (Webb 2000). NTI measures the standardized effect size of the MNTD and is defined as follows (Webb 2000): $NTI = -1 \times (MNTD_{\text{observed}} - MNTD_{\text{randomized}}) / (sdMNTD_{\text{randomized}})$, where $MNTD_{\text{observed}}$ is the observed MNTD, $MNTD_{\text{randomized}}$ is the average MNTD from 999 randomly generated assemblages and $sdMNTD_{\text{randomized}}$ is the standard deviation of the $MNTD_{\text{randomized}}$. NRI was calculated using the same formula by replacing MNTD with MPD. The positive NRI/NTI indicates that co-occurring species are more phylogenetically related (phylogenetic clustering) than expected by chance, whereas the negative value indicates that species are more distantly related (phylogenetic overdispersion) than expected by chance (Webb 2000). Both NRI and NTI were calculated based on both presence/absence and abundance data by using R package *picante* (Kembel *et al.* 2010).

Environmental variables

Forest microclimate has a critical effect on plant diversity and their distributions (Suggitt *et al.* 2017). At each plot, air temperature and relative humidity were recorded 1 m aboveground using a data logger (iButtons DS1923#F5; Maxim Integrated Products, Inc., TX) placed under a solar radiation shield, and soil temperature was monitored 10 cm belowground using another data logger (iButtons DS1922L#F5; Maxim Integrated Products, Inc., TX). All climate data were recorded

in 2-h intervals. In this study, we used the average values of air temperature, relative air humidity and soil temperature during the growing seasons (June–August) collected during 2018–2019.

In addition to the climate data, the slope and the aspect were measured at the center of each plot using a clinometer and a compass, respectively. Cosine transformation of the aspect was used for linear models (Legendre *et al.* 2009). A Trimble RTK (Real-Time Kinematic) GPS with an accuracy of <1 m was used to obtain the elevation for each plot. Stand basal area was used as a predictor of local-scale tree competition in our study since it represents the average resource availability for the individuals within a plant community (Biging and Dobbertin 1992; Zhang *et al.* 2015).

Statistical analysis

Simple linear and quadratic regression models were used to explore the relationship of species richness, Shannon–Wiener index, MPD, MNTD, abundance-weighted MPD and abundance-weighted MNTD with elevations. The same approaches were used to investigate beta diversity patterns.

To disentangle the mechanisms driving plant diversity and community assembly, we first used Pearson's correlation to analyze the relations between environmental variables and alpha diversity and phylogenetic structure. Second, spatial linear model (SLM) was used to assess the relative roles of the environmental variables in shaping patterns of alpha diversity and community structure. For SLM, the spatial simultaneous autoregressive error models were used to consider the effects of spatial autocorrelation (Kissling and Carl 2008). Moran's I values were calculated with the nearest neighbor in R package *spdep* (Bivand *et al.* 2019). To avoid the potential influence of the multicollinearity, the elevation was excluded from this analysis because it was highly correlated with several climatic variables. For each analysis, all the possible combinations of abiotic and biotic variables were used to fit the models. The selection of the 'best' model was based on the minimization of Akaike's information criterion (AIC) and the relative importance of all environmental variables were quantified by the summed AIC weights across all possible models (Zhang *et al.* 2013). Finally, the explanatory power of predictor variables were evaluated on beta diversity with simple Mantel tests using R package *vegan* (Oksanen *et al.*

2017). In addition, distance-based redundancy analysis on each dissimilarity matrix was used to evaluate community–environment relationships. All the geographical and environmental distances were calculated using the Euclidean distance. All statistical analyses were conducted in R language v3.5.3 (R Core Team 2019).

RESULTS

Taxonomic and phylogenetic diversity patterns

Considering species abundance or not had inconsistent effects on taxonomic and phylogenetic alpha diversity patterns (Fig. 2). Species richness and Shannon–Wiener index increased with elevation ($R^2 = 0.284$ and 0.277 , respectively; $P < 0.05$ for both), and both of them tended to decrease at the highest elevation (Fig. 2a and b). For phylogenetic alpha diversity, no relationship was detected between MPD and elevation (Fig. 2c), while abundance-weighted MPD was positively correlated with elevation ($R^2 = 0.268$, $P < 0.05$, Fig. 2d). MNTD decreased monotonically with increasing elevation ($R^2 = 0.392$, $P < 0.01$, Fig. 2e), whereas abundance-weighted MNTD showed no clear trend (Fig. 2f).

The presence-based and abundance-based dissimilarity measures in species composition and phylogenetic relatedness showed overall similar patterns along elevation (Fig. 3). However, taxonomic and phylogenetic beta diversity differed in their relations with elevation. Taxonomic beta diversity increased as elevational distance increased, and remained stable after the distance reached around 800 m (Fig. 3a and b). For phylogenetic beta diversity, the presence-based and abundance-weighted β_{MPD} showed hump-shaped patterns (Fig. 3c and d), whereas presence-based and abundance-weighted β_{MNTD} were consistently increased along increased elevational distances (Fig. 3e and f).

Phylogenetic structure of plant community

There was no linear trend on community phylogenetic clustering or overdispersion along elevation based on all the measures of phylogenetic relatedness (Fig. 4). Plant communities tended to be phylogenetically overdispersed at low (300–500 m) and higher (1000–1300 m) elevations, and clustered trends were detected at middle elevations (500–1000 m) and the mountain top (>1300 m). In addition, several plots had contrast phylogenetic

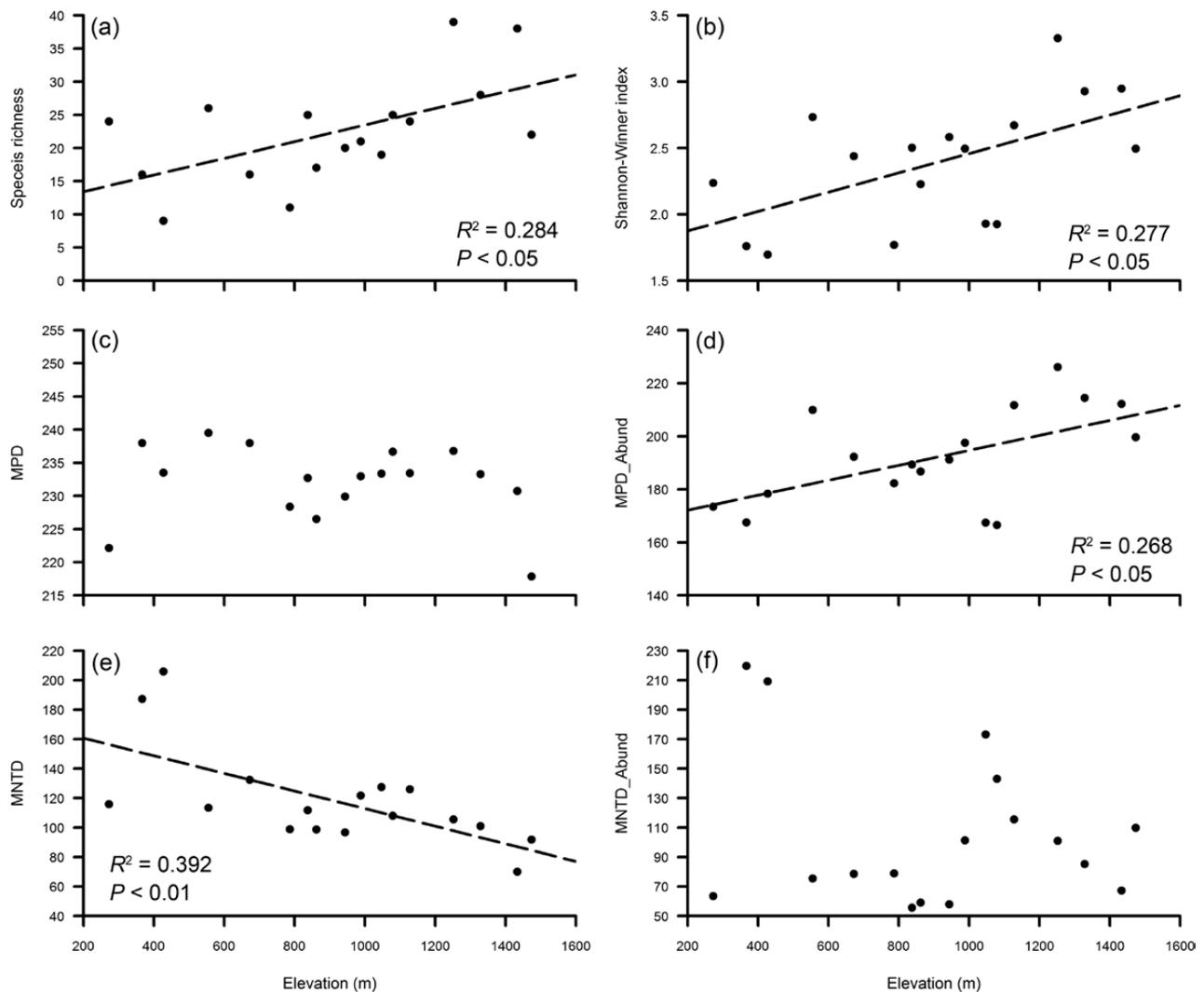


Figure 2: The relations between elevation and the taxonomic alpha diversity (a, b) and phylogenetic alpha diversity (c–f) along the elevational gradient. Only significant trends ($P < 0.05$) were fitted. Abbreviations: MNTD_Abund = abundance-weighted MNTD, MPD_Abund = abundance-weighted MPD.

structure when using the abundance-weighted and unweighted measures (Fig. 4).

Determinants of plant diversity and community structure

For taxonomic alpha diversity, the aspect, the slope, stand basal area and air temperature were identified as the main drivers (Table 1; Supplementary Table S1). For phylogenetic alpha diversity, MPD and MNTD were significantly associated with topographical and climatic variables, while stand basal area played a supplementary important role in shaping abundance-weighted measures (Table 1). Taxonomic and phylogenetic beta diversity were significantly and positively correlated with differences in elevational

distance, air temperature, soil temperature and the slope (Table 2; Supplementary Fig. S1).

The topographic and climatic variables had high explanatory power for phylogenetic structure of plant community (Table 1; Supplementary Table S1). Taking species abundance into account, the relations between the environment and phylogenetic structure varied largely. NRI was negatively correlated with soil temperature, whereas abundance-weighted NRI was positively correlated with the aspect and the slope. NTI was significantly negatively related to air temperature, while abundance-weighted NTI was strongly and positively related with the slope and negatively correlated with air temperature.

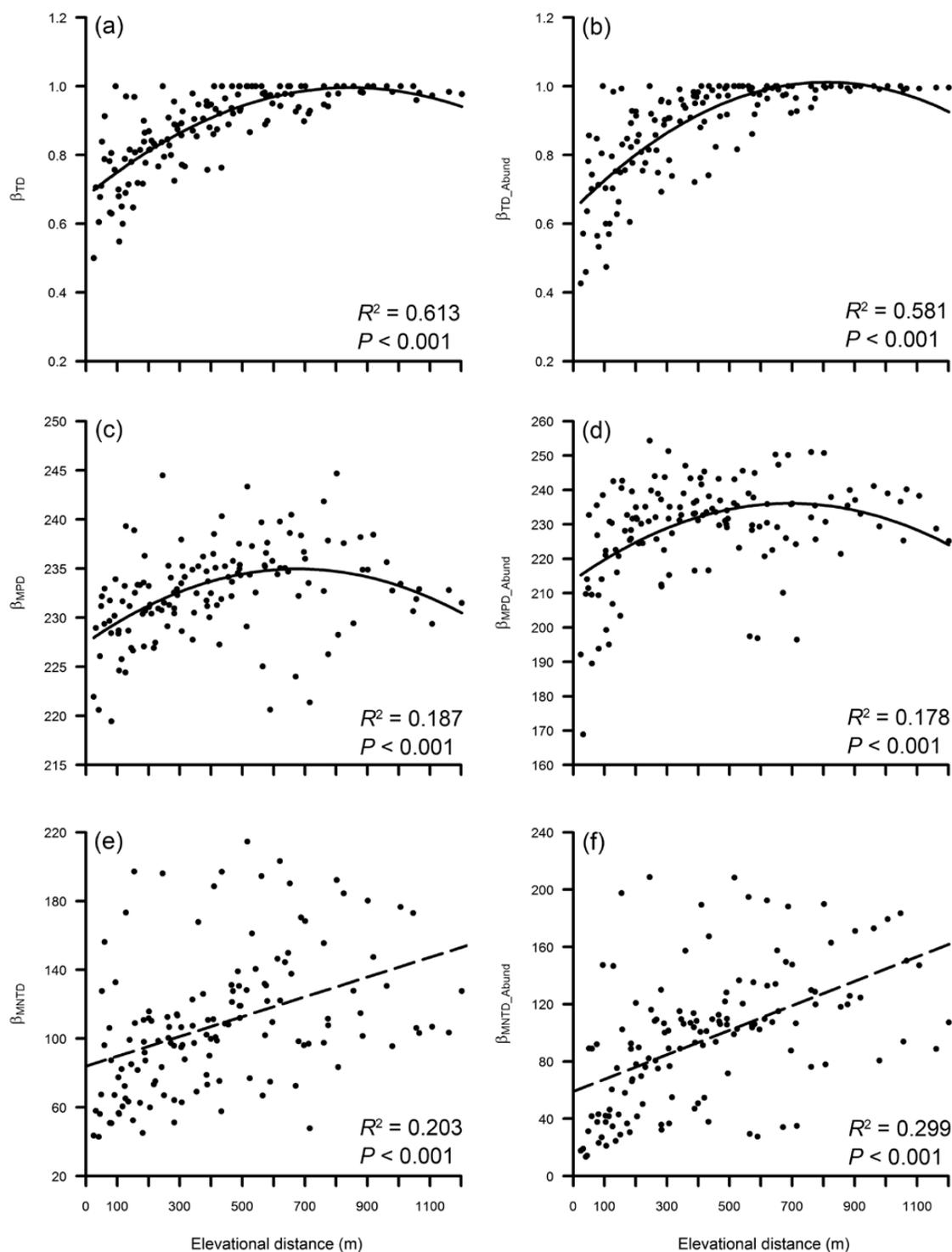


Figure 3: The relations of elevational distance with species compositional dissimilarity (a, b) and phylogenetic dissimilarity (c–f). Only significant trends ($P < 0.05$) were fitted. Abbreviations: β_{MPD} and β_{MNTD} = phylogenetic dissimilarity derived from presence-based MPD and MNTD, β_{MPD_Abund} and β_{MNTD_Abund} = phylogenetic dissimilarity derived from abundance-weighted MPD and MNTD, β_{TD} = presence-based taxonomic dissimilarity, β_{TD_Abund} = abundance-weighted taxonomic dissimilarity.

DISCUSSION

In this study, we combined plant diversity data and fine-scale environmental variables to analyze

the changes of plant diversity and community phylogenetic structure along an elevational gradient and explore the underlying abiotic and biotic drivers in subtropical forests in eastern

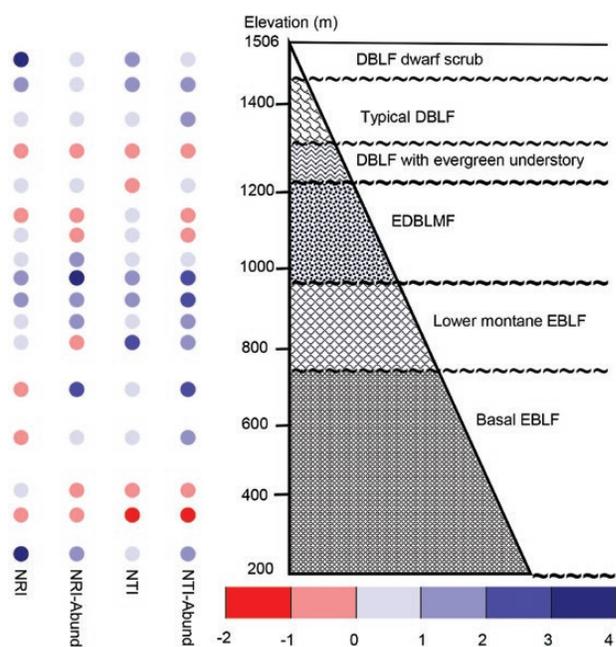


Figure 4: Variations in community phylogenetic relatedness along the elevational gradient. Positive values (blue points) indicate phylogenetic clustering, while negative values (red points) indicate phylogenetic overdispersion. The large triangle on the right represents the vegetation distributions on Mt. Tianmu according to [Da et al. \(2009\)](#). Abbreviations: DBLF = deciduous broad-leaved forest, EBLF = evergreen broad-leaved forest, EDBLMF = evergreen and deciduous broad-leaved mixed forest. Other abbreviations are described in [Table 1](#).

China. By incorporating the information of species abundance, we found that species abundance provides novel insights for understanding plant community assembly ([Cadotte et al. 2010](#)). Unlike taxonomic alpha diversity, phylogenetic alpha diversity yielded inconsistent patterns when the abundance information was included ([Fig. 2](#)). The uneven distributions of plant species abundance along elevations contribute to the explanation of these changes ([Chao et al. 2014](#); [Tucker and Cadotte 2013](#)). There were marked differences in the plant abundance at different elevations. For example, the genus *Quercus* had much higher abundance at low and middle elevations compared with that at high elevations. At high elevations (>1200 m), 476 (~60%) of the 806 plant individuals belonged to six closely related genus such as *Cornus* and *Hydrangea*, while the remaining individuals belonged to other 34 genus. Furthermore, abundance-weighted MPD and MNTD had opposite relations with the slope. Generally, MPD captures distant evolutionary events ([Ricklefs 2006](#)), while MNTD is influenced by relatively recent adaptations ([Mazel et al. 2016](#); [Webb 2000](#)). In Mt.

Tianmu, the forests at middle elevations with steep topography were mainly composed of six distantly related genus such as *Quercus* and *Symplocos*, with a large proportion of the plant individuals belonged to these genus, leading to relatively high MPD in these plots. In contrast, species abundance provided little information to explore the drivers shaping both taxonomic and phylogenetic beta diversity. The differences in temperature, elevation and slope were significantly correlated with the turnover in species and phylogenetic composition of plant communities, indicating the importance of abiotic sorting and dispersal limitation in community assembly in subtropical forests ([Culmsee and Leuschner 2013](#)).

It is somewhat surprising that plant taxonomic alpha diversity increased along elevation but decreased at the mountaintop of Mt. Tianmu. Generally, unimodal or monotonically decreasing patterns of species richness along elevations were widely reported in previous studies. [Rahbek \(2005\)](#) did a meta-analysis for 204 studies of elevational patterns in biodiversity, and found that nearly 50% of the recorded patterns were unimodal, around 25% followed a monotonic decline, and less than 10% were increasing patterns (see [Figure 3](#) in [Rahbek \(2005\)](#) for the detail). A similar result was documented based on an updated meta-analysis for 443 studies by [Guo et al. \(2013\)](#). Two reasons may contribute to the observed pattern of plant species in Mt. Tianmu. One is that the extent of an elevation gradient sampled may have a pronounced impact on the patterns ([Guo et al. 2013](#); [Nogués-Bravo et al. 2008](#)). Mountains with long elevational extents (>1000 or 2000 m) show proportionally more unimodal patterns ([Guo et al. 2013](#); [Rahbek 2005](#)), while shortened gradients often represent insufficient variations in environmental conditions that could result in highly variable patterns ([Itow 1991](#)). Although our study sites have covered the nearly entire elevational range (~300–1500 m) of the mountain, the changes in vegetation types along elevation are not dramatic compared with some other mountains in southwestern China. The other reason is that human activities increased markedly in last four decades in eastern China ([Zhao et al. 2015](#)), which could have both negative and positive effects on montane biodiversity through local extinction of native species and the increase of nonnative species ([Vellend et al. 2017](#); [Xu et al. 2019](#)). According to recent flora surveys, there are over 200 cultivated plant species recorded in Mt. Tianmu, most of which are distributed in low or middle elevations ([Ding](#)

Table 1: The results of SLM with taxonomic and phylogenetic alpha diversity and phylogenetic structure indices as response variables, and environmental variables as predictors

Environmental variable	Species richness		Shannon-Wiener index		MPD		MPD_Abund		MNTD		MNTD_Abund		NRI		NRI_Abund		NTI		NTI_Abund	
	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W	Coef.	W
Aspect	0.539***	0.996	0.943***	1.000	0.390**	0.652	0.904***	0.682	—	0.306	—	0.298	—	0.407	0.308	0.566	—	0.363	—	0.297
Slope	—	0.277	0.430***	0.999	—	0.346	0.507***	0.954	-0.488**	0.870	-0.947***	0.998	—	0.300	0.421*	0.725	—	0.297	1.050***	0.981
Stand basal area	-0.571***	0.994	-0.953***	1.000	—	0.314	-1.009***	0.605	—	0.347	0.264*	0.520	—	0.309	—	0.325	—	0.372	—	0.394
AirTemp	-0.389*	0.820	-0.720***	0.999	—	0.373	-0.647***	0.919	0.886***	0.892	0.712***	0.936	—	0.368	—	0.302	-0.517*	0.707	-0.456***	0.900
AirHumidity	—	0.332	—	0.441	0.776***	0.719	—	0.347	—	0.420	0.375*	0.532	—	0.465	—	0.331	—	0.393	—	0.428
SoilTemp	-0.289*	0.706	—	0.365	0.602***	0.766	—	0.291	—	0.424	—	0.344	-0.577**	0.720	—	0.289	—	0.470	—	0.404

Coef. is the standardized regression coefficient, indicating the relative importance of variables in the optimal model; W is the summed AIC weights for each predictor across all possible models. Abbreviations: AirHumidity = the average air relative humidity in the growing season, AirTemp = the average air temperature in the growing season, MNTD_Abund = abundance-weighted MNTD, MPD_Abund = abundance-weighted MPD, NRI_Abund = abundance-weighted NRI, NTL_Abund = abundance-weighted NTL, SoilTemp = the average soil temperature in the growing season. Significance levels are * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

2010). Although we tried to avoid the influence of human disturbance by selecting relatively typical vegetation in each elevation range, it is impossible to completely exclude the potential impact of human disturbance in this study. Further studies are urgently needed to monitor and evaluate human impacts in biodiversity along elevational gradients (Peters *et al.* 2019).

Different from several comparative studies reported consistent patterns between taxonomic and phylogenetic alpha diversity of plant species in mountains (e.g. Dossa *et al.* 2013; Mwaura and Kaburu 2009; Qian *et al.* 2014), we found the inconsistent patterns for taxonomic and phylogenetic alpha diversity in Mt. Tianmu. One main reason is the use of different measures in phylogenetic alpha diversity. While Faith's phylogenetic diversity was widely used as the measures of phylogenetic alpha diversity (Faith 1992), this index cannot exclude the effect of species pool (Tucker and Cadotte 2013) as it is usually correlated closely with species richness (Chun and Lee 2017; Gerhold *et al.* 2008; Qian *et al.* 2014). To accurately evaluate the relationship between phylogenetic alpha diversity and elevation, we used MPD and MNTD to decouple from the influence of species richness (Kembel *et al.* 2010). Although plant richness tended to increase with elevation, MNTD showed a decreased elevational pattern, which could be explained by more closely related terminal species at high elevations compared with that at low elevations. In Mt. Tianmu, abundance-weighted MPD increased with elevation, while abundance-weighted MNTD showed no clear trend with elevation. This result was inconsistent with Worthy *et al.* (2019) that reported decreasing abundance-weighted MPD and MNTD for tree communities along an elevational gradient (2440–3330 m) in Ecuador. One possible reason for the inconsistency is the difference in field sampling standards. Worthy *et al.* (2019) only surveyed tree individuals with ≥ 5 cm DBH, while we included all woody plants with ≥ 1 cm DBH. This could lead to huge differences in species richness and abundance, especially in high elevations. For example, in the four plots at >1200 m in elevation in Mt. Tianmu, a majority of species are shrub species and only one-quarter of individuals had the DBHs larger than 5 cm. Therefore, a set of ecologically meaningful and best-practice standards in biodiversity measures and the coordinated field survey methods in biodiversity monitoring should be developed in biodiversity studies along elevational gradients.

Table 2: The results of simple Mantel tests showing the effect of environmental distances on taxonomic and phylogenetic beta diversity along the elevational gradient

Environmental distances	β diversity					
	β_{TD}	β_{TD_Abund}	β_{MPD}	β_{MPD_Abund}	β_{MNTD}	β_{MNTD_Abund}
Elevation	0.740***	0.701***	0.530***	0.490***	0.555***	0.696***
Aspect	-0.014	0.012	0.107	-0.034	0.059	-0.001
Slope	0.222*	0.169*	0.236*	0.193*	0.168*	0.132
Stand basal area	0.114	0.150	0.144	0.009	0.062	0.030
AirTemp	0.538***	0.478***	0.365**	0.309*	0.302	0.406*
AirHumidity	-0.113	-0.093	-0.212	-0.212	-0.039	-0.130
SoilTemp	0.557***	0.518***	0.481***	0.398**	0.521***	0.573***

Abbreviations: β_{MPD} and β_{MNTD} = phylogenetic dissimilarity derived from MPD and MNTD, β_{MPD_Abund} and β_{MNTD_Abund} = phylogenetic dissimilarity derived from abundance-weighted MPD and MNTD, β_{TD} = taxonomic dissimilarity, β_{TD_Abund} = abundance-weighted taxonomic dissimilarity. The abbreviations for the environmental variables are described in Table 1. Significance levels are * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Phylogenetic structure of plant communities varies markedly along elevational gradients and provides insights into the relative importance of different ecological and evolutionary processes (Webb *et al.* 2002). For example, increased phylogenetic clustering at high elevations with low temperature was the evidence for the influence of environmental filtering for plant community assembly in Mt. Changbai in northern China (Qian *et al.* 2014), Mt. Rausu in Japan (Kitagawa *et al.* 2018) and European Alps (Marx *et al.* 2017). In contrast, angiosperm woody species were distantly related to each other at high elevations and were often hypothesized as the results of biotic interactions for community assembly in Mt. Baekhwa in South Korea (Chun and Lee 2017) and the Rocky Mountains in USA (Bryant *et al.* 2008). In our study, plant communities tended to be phylogenetically overdispersed at low and high elevations and clustered at middle elevations. Phylogenetic relatedness was strongly correlated with air temperature, soil temperature, the slope and the aspect, suggesting that environmental filtering was the main driver for plant communities along the gradient. Biotic interactions using stand basal area as the proxy had no significant correlation with the four measures of phylogenetic structure, suggesting the weak effect of competitive exclusion. Since phylogenetic distantly related species within plant communities may independently evolve similar traits to adapt to similar environments via convergent evolution, we still observed the

overdispersed phylogenetic structure in the lack of evidence of competitive exclusion in several sites (Cavender-Bares *et al.* 2009; Webb *et al.* 2002).

Plant diversity and phylogenetic structure in Mt. Tianmu were strongly associated with fine-scale air temperature and soil temperature. Microclimate can be highly heterogeneous and strongly divergent from surrounding environments, and thereby influence forest biodiversity and community structure (Ohler *et al.* 2020; Potter *et al.* 2013). Opedal *et al.* (2015) found that small-scale variation in temperature and soil moisture allowed plant species to escape from regional climate change by providing local microrefugia. Soliveres *et al.* (2012) reported that microclimatic conditions affected the phylogenetic structure of understory species through environmental filtering for grassland communities in Spain. According to the microclimate data we collected in last 2 years in the 17 sites, significant variations were observed in air and soil temperature along elevations and among seasons. For example, the diurnal variation of soil temperature in growing seasons varied from 0 to 11.3 °C, and the daily temperature difference between air and soil for the same sites ranged from 0 to 8.9 °C. As we reported in this study, these variations in microclimate could have a dramatic influence on plant diversity and composition by adjusting plant survival, growth and mortality at local scales (Chen *et al.* 1999; Dingman *et al.* 2013; Porter and Gates 1969). However, due to the lack of microclimate data in most studies on elevational

biodiversity (De Frenne and Verheyen 2016), the effects of microclimate on plant diversity and community structure have been assumed rather than directly tested (Jucker *et al.* 2020). Toward a comprehensive understanding of plant community assembly, further studies are needed to evaluate the role of microclimatic variables (e.g. seasonal and diurnal variations in air and soil temperature and moisture) in plant community composition and dynamics (Körner and Hiltbrunner 2018).

In conclusion, this study showed that both ecological and evolutionary explanations are necessary to understand elevational biodiversity gradients, and the incorporation of species abundance into the measures of biodiversity and community structure, as well as the consideration of fine-scale microclimate, can provide novel insights for understanding plant community assembly along elevations. The emergence of the different patterns and their underlying mechanisms is probably caused by the differences in taxonomic groups, local environmental conditions and sampling efforts among different studies. Further studies in microclimate and plant functional traits across different mountains are needed toward a deep understanding of the mechanisms driving current biodiversity patterns along elevational gradients.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Pearson's correlations between abiotic and biotic variables with alpha diversity and the measures of community phylogenetic structure.

Figure S1: Distance-based redundancy analysis (db-RDA) of taxonomic beta diversity (a, b) and phylogenetic (c–f) beta diversity and environmental variables.

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