

1 Identifying the patterns of changes in α and β diversity across

2 *Dacrydium pectinatum* communities in Hainan Island, China

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16 Abstract

17
18 Exploring vegetation distribution spatial patterns facilitates understanding how biodiversity
19 addresses the potential threat of future climate variability, especially for highly diverse and
20 threatened tropical plant communities, but few empirical studies have been performed over various
21 environmental scales. In this study, we used species-based and phylogeny-based methods to analyze
22 the α - and β -diversity pattern variation in *Dacrydium pectinatum* communities and its key drivers
23 along elevation and geographical gradients across three national nature reserves in Bawangling,
24 Diaoluoshan and Jianfengling. Our study indicates that the species and phylogenetic α -diversity
25 patterns presented consistent decreasing with elevation, with the peak occurring at low elevations.
26 Environmental filtering caused by decreases in limiting factors, such as temperature, precipitation,
27 soil organic matter, soil phosphorus, and light, is the main reason for the decline in diversity at high
28 elevations, whereas low-elevation areas are affected by various factors, such as environmental
29 filtering and similarity limitations. Species and phylogenetic β -diversity changes are closely related
30 to environmental filtering and dispersal limitation, but the latter is key in community assembly at
31 the heterogeneous spatial scale. In conclusion, combining species-based and phylogeny-based
32 methods to explore the biogeographic patterns of tropical plant communities helps provide
33 convincing evidence and confirms that the relative contributions of niche and neutral theory in the

assembly process vary along environmental gradients. Though the *D. pectinatum* community constitute a floristically integrated unit, the genetic relationships between species are relatively far, and co-evolution to promote species coexistence is difficult when faced with habitat pressure. Hence, we believe that species coexistence in tropical plant communities requires mild environmental conditions, and low temperatures, precipitation, soil nutrients and light will aggravate environmental filtering and species competition. We also recommend strengthening the construction and management of nature reserves and the exploration of biodiversity formation mechanisms, which are crucial for biodiversity conservation in endangered tropical plant communities.

Keywords Biodiversity hotspots, *Dacrydium pectinatum*, deterministic processes, stochastic processes, α and β diversity, Hainan Island

1. Introduction

One of the central themes in ecology is understanding the spatial patterns in biodiversity along various environmental axes (Bagchi et al., 2011). This understanding helps address the looming threats to biodiversity by contributing to regional-scale biological conservation activities, such as reserve design and habitat restoration (Mori et al., 2013). In recent years, more than 100 hypotheses have been proposed to explain biodiversity patterns at the community level (Ricklefs, 2004). Two of the most widely discussed hypotheses pertain to niche-based deterministic and neutrality-based stochastic processes (Wright, 2002). In deterministic processes, limiting similarity, such as through competition, facilitation, and predation, and environmental filtering, including through energy availability, water availability, energy-water balance, and habitat heterogeneity, plays a key role (O'Brien et al., 2000, Qin et al., 2017). In contrast, neutral processes emphasize the great roles of stochastic immigration and mortality in community assembly, with the actual level of species richness determined by the size of the regional species pool (Rosindell et al., 2011). Based on the assumption of dispersal limitation, the similarity between communities is expected to decrease with increasing spatial distance, and this decreasing pattern is related only to geographical distance rather than the influence of environmental factors (Tang et al., 2012).

Strong evidence indicates the existence of both significant variation and a large degree of overlap in microhabitat preferences among species in diverse subtropical and tropical forests (Kraft et al., 2008, Lai et al., 2009), and species with similar microhabitat requirements often spatially overlap with each other (Song et al., 2018). Additionally, studies have shown that plant species in

68 communities tend to show stronger competition, and microhabitat preference usually corresponds to
69 a narrower spatial scale (Willis et al., 2009); however, changes in geography and the environment,
70 as well as other spatial factors, have gradually enhanced the assembly effect of the community as
71 the spatial distance has increased (Chave, 2004). Hence, the local-scale diversity patterns addressed
72 by niche theory might be insufficient for explaining the complex structure of tropical plant
73 communities (Wang et al., 2016). There is a current interest in merging niche and neutral theory to
74 explain the biogeographical patterns of diversity (Alonso et al., 2006, Adler et al., 2007), which will
75 help eliminate some key flaws in niche theory, such as diffuse restrictions and stochastic
76 immigration during the process of community assembly (Etienne and Alonso, 2005). Exploring the
77 relationship between β diversity and environmental differences and geographic distance is an
78 effective way to reveal how biodiversity varies along environmental axes (Chesson, 2000). The
79 most widely recognized spatial patterns are the gradients that occur with elevation and latitude
80 (Jiménez-Alfaro et al., 2014, Molina-Venegas et al., 2020). Knowledge of these patterns is also
81 critical for predicting how global climate change will affect future biodiversity distributions (Jiang
82 et al., 2016), as most species are expected to be forced to shift their distributions to higher
83 elevations/latitudes in a warmer future (Mori et al., 2013, Molina-Venegas et al., 2019).

84 Traditional species diversity emphasizes equality among species while ignoring the
85 evolutionary differences across diverse species (Graham and Fine, 2008). However, phylogenetic
86 biology currently uses the close associations between species to speculate on the mechanisms of
87 community assembly, which helps bridge the gap between evolutionary and community ecology
88 (Kraft and Ackerly, 2010). Ecologists generally believe that closely phylogenetically related species
89 are more functionally similar compared to distantly related species (Swenson et al., 2007, Xu et al.,
90 2017). Nevertheless, limiting similarity might lead to phylogenetic overdispersion among
91 coexisting species, allowing them to compete with each other for finite resources (Webb, 2000). In
92 contrast, environmental filtering may cause the accumulation of some species with similar niche
93 characteristics, thus forming a convergence pattern in phylogenetic distances (Kraft et al., 2008).
94 Additionally, if neutral processes drive community assembly, phylogenetic structures usually
95 exhibit a randomized distribution (Cornwell and Ackerly, 2009). However, some researchers have
96 come to the opposite conclusion that phylogenetic patterns may have limited use as proxies of
97 community assembly, showing that the phylogenetic dispersion of communities is of limited value
98 for understanding ecological assembly processes and can only be used to reveal the
99 macroevolutionary idiosyncrasies of the habitat of their associated lineage-pool (Gerhold et al.
100 2015). These contradictory results indicate that correctly identifying the assembly patterns of
101 communities remains a major challenge for ecologists. Hence, to achieve a mechanistic view of the

community assembly process along environmental gradients, researchers should simultaneously analyze phylogeny and traditional measures of species diversity.

Despite substantial efforts, until now, the underlying drivers of the spatial organization of diversity in tropical plant communities has remained difficult to generalize (Mokany et al., 2011). For instance, environmental filtering was found to be the main factor driving community assembly during succession in a tropical forest in New Guinea (Whitfeld et al., 2014). However, some studies have also supported the idea of incomplete filtering (Song et al., 2019), showing that geographical and environmental factors jointly contribute to the community assembly process in tropical forests (Zhang et al., 2013). Given these contrasting results, there is still much to learn about the mechanism of biodiversity formation in the tropics. Hence, clarifying the spatial distribution patterns of various diversity indicators, such as plant composition/diversity and phylogenetic structures, helps reveal the biogeographic patterns, assembly processes, and mechanisms of the formation of biodiversity. It may also provide a scientific basis for the proper management, sustainable utilization and sound conservation of resources in different vegetation types.

Hainan Island in China is floristically rich and has been listed as an internationally significant biodiversity conservation area (Myers et al., 2000). Based on current records, approximately 4,600 woody plants have been recorded, and 397 of these plants are endemic to the island (Francisco-Ortega et al., 2010). In this manuscript, we used species-based and phylogeny-based methods to analyze the variation in the structure of *Dacrydium pectinatum* communities across three highly diverse national nature reserves in Bawangling, Diaoluoshan, and Jianfengling on Hainan Island, China (Fig. 1), which have different climatic and geographical features and are the main distribution zones of *D. pectinatum*. Specifically, our objectives were to (1) explore the distribution patterns and environmental determinants of species and phylogenetic α diversity at different spatial scales, (2) clarify the change patterns of species and phylogenetic β diversity and assess the degree to which species composition variation may be explained by the elevation distance, geographical distance and environmental gradients, and (3) based on these findings, understand and reveal the assembly process of the *D. pectinatum* plant community. We expect that the results of this study will increase our understanding of the biodiversity-formation and -conservation mechanisms of tropical plant communities on Hainan Island, China.

2. Materials and methods

2.1 Study sites

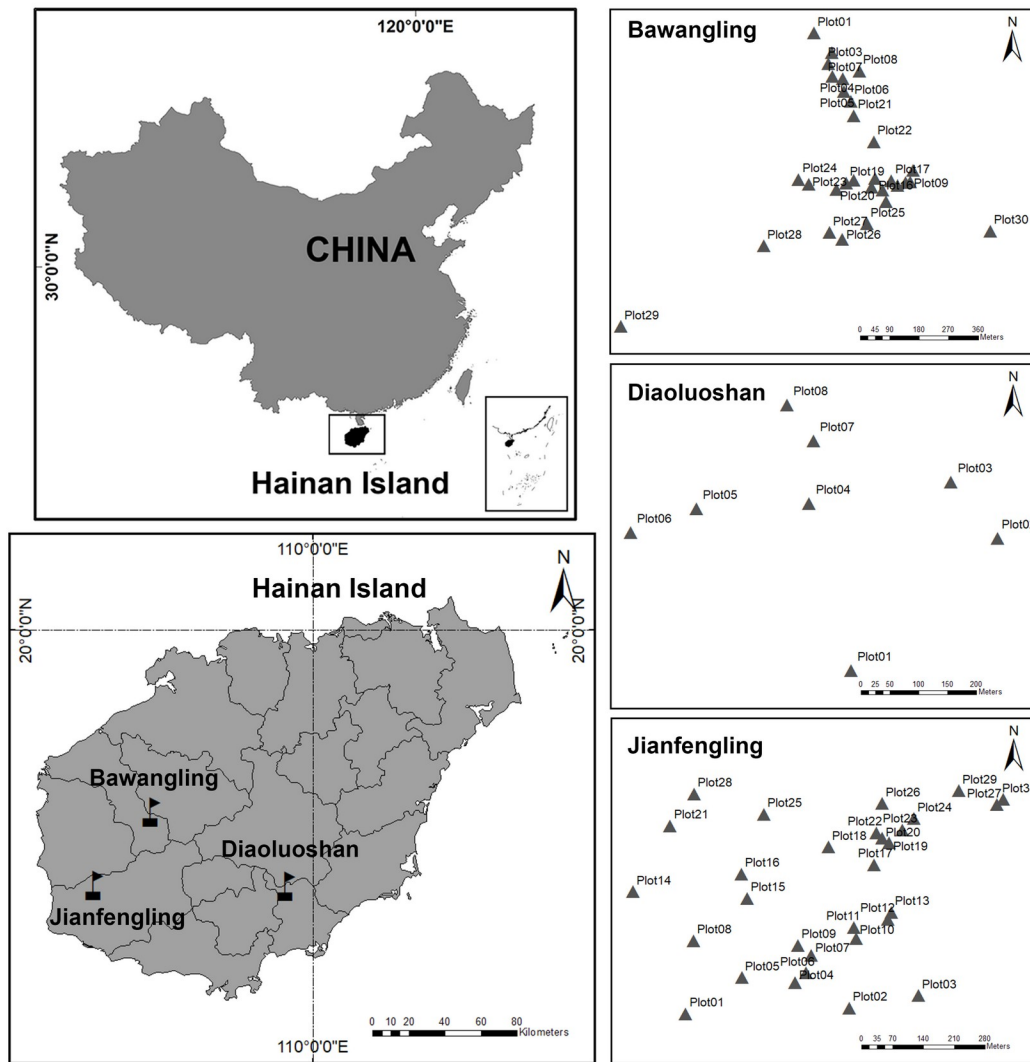


Fig. 1 Permanent plot locations in the natural *D. pectinatum* communities in the three national nature reserves of Bawangling, Diaoluoshan and Jianfengling, Hainan Island, China.

Hainan Island is located in southeastern China (18.14°-20.02°N, 108.62°-111.05°E) on the northern edge of tropical Asia. The topography is higher in the middle than around the edges of the island. The average annual precipitation is 923-2459 mm and decreases from east to west, and the annual average temperature is 22.5-25.6 °C and decreases from south to north. The southwest and west are affected by ocean monsoons, and there are obvious wet and dry seasons. More clouds and lower temperatures occur in the central mountainous region than elsewhere on the island.

Dacrydium pectinatum is one of the constructive and endangered species in the tropical mountain forests of Hainan Island and belongs to the *Podocarpaceae* family (Keppel et al., 2011). Its modern distribution in the Northern Hemisphere is limited to approximately 20°N south, and it appears to have become extinct in Australia during the Miocene (Norton et al., 1988). *D.*

150 *pectinatum* is the only species of its genus that exists in China and is found only in four original
151 tropical rainforests on Hainan Island, namely, Bawangling, Jianfengling, Diaoluoshan and
152 Wuzhishan (Huang et al., 2014). In addition, according to our previous investigation, the natural
153 community shaped by this species as an absolute dominant tree species has high diversity (Wu et
154 al., 2019). The current study was conducted in Bawangling, which is located in the southwestern
155 part of Hainan Island (18°53'-19°20'N, 108°58'-109°53'E), Diaoluoshan, which is situated in the
156 southeastern part of Hainan Island (18°43'-18°58'N, 109°43'-110°03'E), and Jianfengling, which is
157 located in the southwestern part of Hainan Island (18°23'-18°50' N, 108°36'-109°05'E). These areas
158 are national nature reserves in China (Fig. 1).

159 The total area of the Diaoluoshan Nature Reserve is approximately 37,900 hm², and it was
160 established in 1994. The reserve has a marine tropical monsoon climate. The annual mean
161 temperature is 24.4 °C, and the annual mean precipitation is 1870-2760 mm. The topography is
162 high in the northwest and low in the southeast, and the elevation ranges between 50 and 1,499 m.
163 The soil types are mainly mountain yellow soil and mountain red soil. The forest vegetation types in
164 the region are mainly tropical secondary forest, tropical monsoon forest, and tropical evergreen
165 broad-leaved forest, among which 1955 species of vascular plants in 194 families and 870 genera
166 have been recorded (Wang et al., 2007).

167 The total area of the Bawangling Nature Reserve is approximately 72,000 hm², and it was
168 established in 1980. The reserve has a tropical monsoon climate. The annual mean temperature is
169 23.6 °C, the annual mean precipitation is 1500-2000 mm, and the average relative humidity is 65-
170 90%. The topography is mainly mountainous, and the elevation ranges between 100 and 1,654 m.
171 The soil type is mainly brick-red soil formed by granite and sandstone. The vegetation types are
172 mainly low mountain rainforest, gully rainforest and mountain rainforest, among which 2213
173 species of vascular plants in 220 families and 967 genera have been recorded (Long et al., 2011).

174 The total area of the Jianfengling Nature Reserve is approximately 640 km², and it was
175 established in 1960. The reserve has a monsoon climate of tropical islands at low latitudes. The
176 annual average temperature decreases from 25 to 17-19 °C, and the annual precipitation increases
177 from 1300 to 3500 mm along a horizontal distance of approximately 15 km from the coast to the
178 highest elevation of the forest hinterland (the elevation range is 200 to 1,412 m.). Coastal areas are
179 dominated by coastal sandy soil, dry red soil, brick-red soil, and brick-yellow soil. The highest
180 mountain areas mainly have leached-surface latent yellow soil. The vegetation types in the region
181 include tropical semideciduous monsoon rainforest, tropical evergreen monsoon rainforest, coastal
182 barbed scrub, savanna, and dwarf moss forest on the top of the mountain, among which 2258
183 species of vascular plants have been recorded (Xu et al., 2013).

The detailed coordinate, climate and topography data for the three study sites are shown in Table 1 (elevation data from field records). The climate data, including the annual mean temperature and the annual precipitation, were extracted from the information on the current conditions (1950–2000) in the WorldClim global climate database (<http://www.worldclim/>).

Table 1 Topographic and climatic characteristics across the three *D. pectinatum* communities

Forest type	Latitude	Longitude	Elevation	Temperature	Precipitation
BWL					
TMRF	18°57'N	109°03'E	1155.78±56.93 ^b	20.74±1.78 ^a	1617.76±116.52 ^b
DLS					
TMRF	18°43'N	109°43'E	935.97±22.96 ^a	21.89±1.60 ^b	1806.73±98.13 ^c
JFL					
TMRF	18°20'N	108°41'E	907.43±46.54 ^a	21.75±1.52 ^b	1520.33±135.14 ^a

TMRF represents tropical mountain rainforest. BWL represents Bawangling, DLS represents Diaoluoshan, and JFL represents Jianfengling. Elevation (m), temperature (°C), and precipitation (mm) are expressed as the mean ± sd.

2.2 Field investigation and plant sampling

Field investigations were conducted from December 2017 to July 2018. Because endangered species mostly occur in low-density populations with small quantities and scattered distributions, the minimum-area sampling method was more suitable for this study compared to the large-scale survey method. We established sixty-eight permanent plots across Bawangling, Diaoluoshan, and Jianfengling. Based on previous surveys and the experience of local forestry workers, we constructed the plots under the following considerations: (1) the plots must contain varying numbers of adult *D. pectinatum* individuals, and *D. pectinatum* must be a top-level plant species; (2) the conditions within the stand must be relatively uniform and show limited human interference; and (3) if the sites meets the above criteria, the plot is randomly established within the stand. We established 30 plots in Bawangling and 30 plots in Jianfengling, each of which had an area of 900 m² (30×30 m). Due to the severe deforestation in Diaoluoshan, we established only 8 permanent plots at this location.

All woody stems (including those of trees, shrubs, and lianas) with a diameter at breast height (DBH) ≥5 cm were identified to the species level, tagged, and mapped, and their DBH was

210 measured. The nomenclature follows that used in the Flora of China (<http://foc.eflora.cn/>). Their
211 health status was recorded (such as living trees, dying trees and dead trees—note that only living
212 trees were quantitatively analyzed in this study), and their height, crown width, branch height and
213 spatial position were measured. In each plot, three twenty-five m² (5×5 m) subplots were also
214 established, and woody stems with a DBH <5 cm were recorded by referring to the above criteria.

215 In total, 52 families, 101 genera, 187 plant species, and 5386 stems; 42 families, 73 genera, 126
216 plant species, and 1023 stems; and 54 families, 110 genera, 186 plant species, and 5705 stems were
217 recorded in Bawangling, Diaoluoshan, and Jianfengling, respectively (Table 2). The number of
218 Lauraceae plants was most abundant, with totals of 10 genera and 24 plant species, 10 genera and
219 16 plant species, and 8 genera and 25 plant species in Bawangling, Diaoluoshan, and Jianfengling,
220 respectively (to see Appendix S1). In addition, we have also listed the top ten species in terms of
221 importance values (IV). Only 7.69% of the families (*Podocarpaceae*, *Fagaceae*, *Magnoliaceae*, and
222 *Polygalaceae*), 14.28% of the families (*Podocarpaceae*, *Fagaceae*, *Hamamelidaceae*, *Theaceae*,
223 *Magnoliaceae*, and *Polygalaceae*), and 7.41% of the families (*Ulmaceae*, *Palmae*, *Podocarpaceae*,
224 and *Lauraceae*) had importance values greater than 2% in Bawangling, Diaoluoshan, and
225 Jianfengling, respectively.

226

227 2.3 Environmental factor measurement

228

229 Soil samples were collected along the diagonal (upper left, middle, and lower right) in each of
230 the 30×30 m plots. A core of the top 20 cm of soil was removed at each point. Soil samples were
231 mixed into a single sample and dried in the laboratory. After sieving, the physical and chemical
232 indicators of the soil samples were measured in accordance with international standard methods.
233 The indicators included the soil organic matter (SOM, g·kg⁻¹, potassium dichromate oxidation
234 volumetric method, LY/T 1237-1999), soil total nitrogen (TN, g·kg⁻¹, Kjeldahl boiling-diffusion
235 method, LY/T 1228-1999), soil total phosphorus (TP, g·kg⁻¹, sodium hydroxide alkaline fusion-
236 molybdenum anti-colorimetric method, LY/T 1232-1999), soil alkaline nitrogen (AN, mg·kg⁻¹,
237 alkaline hydrolysis- diffusion method, LY/T 1229-1999), soil available phosphorus (AP, mg·kg⁻¹,
238 0.05 mol·L⁻¹ HCl-0.025 mol·L⁻¹ 1/2 H₂SO₄ extraction method, LY/T 1233-1999), and soil pH (pH,
239 H₂O 1:2.5 potentiometry, LY/T 1239-1999). In each 30×30 m plot, elevation (EL, m), latitude and
240 longitude data were collected with a global positioning navigation system (GPS). In addition, stand
241 characteristics (e.g., canopy density, CD) and other topographic factors (e.g., aspect, AS; slope
242 aspect, SP; and slope, SL) were also recorded.

243

244 **2.4 Diversity indices**

245

246 **2.4.1 Species α and β diversity**

247

248 In this study, we used the species richness index (SR) as a measure of the species α diversity,
249 which represents the number of species in each plot. To analyze the patterns of the species β
250 diversity along various environmental gradients, the Jaccard index was calculated using the vegan
251 package in R version 3.5.3. The formula for this calculation is as follows (Jaccard, 1912):

252
$$Jaccard = \frac{(b+c)}{(a+b+c)} \quad (1)$$

253 Here, “a” represents the number of cooccurring species in two plots, and “b” and “c” represent the
254 numbers of unique species in the two plots. An increase in the Jaccard index indicates that the
255 difference in species compositions has increased.

256

257 **2.4.2 Phylogenetic tree construction**

258

259 The phylogenetic supertree should be established before phylogenetic diversity analysis.
260 Hence, we used V.PhyloMaker (a freely available package for R) (Jin, Y., & Qian, H. 2019) and the
261 woody plant list (it includes 346 species, 150 genera and 69 families) created from the
262 comprehensive field surveys performed at the three sites for supertree construction. V.PhyloMaker
263 provides an inclusive species-level time-calibrated mega-phylogeny for seed plants, and this mega-
264 phylogeny was used as a backbone to build the phylogenetic supertree (Fig. 2). This procedure
265 shifted the phylogenetic data of the analyses to an optimum level.

266

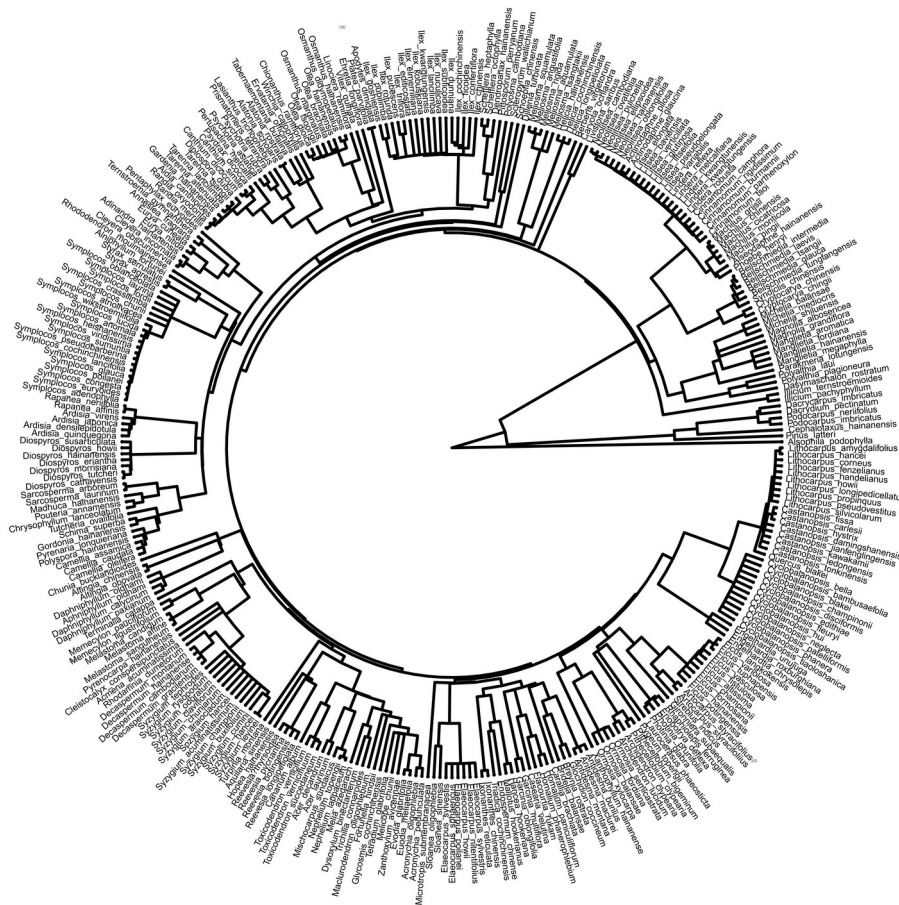


Fig. 2. Phylogenetic tree of *D. pectinatum* communities constructed using the V.PhyloMaker including 344 taxa distributed across 150 genera in 69 families.

2.4.3 Phylogenetic α and β diversity

The statistical analyses and data processing were mainly carried out in R statistical software 3.6.3. Faith's PD (PD) was used as a measure to describe the phylogenetic α diversity, and this value is the sum of the minimum spanning path in the phylogenetic tree connecting all species found in a local plot (Faith, 1992). In recent years, various phylogenetic β diversity measures have been proposed, such as the mean phylogenetic dissimilarity (D_{pw}) between the individuals or species in two communities (Rao, 1982; Webb et al., 2008), the mean nearest taxon distance (D_{nn}) between the individuals or species in two communities (Webb et al., 2002; Webb et al., 2008), and the amount of phylogenetic branch length shared between species in two communities (PhyloSor, Bryant et al., 2008). We used the mean nearest taxon distance (D_{nn}) to assess the phylogenetic β diversity in this manuscript, and the calculation formula is as follows:

$$D_{nm} = \frac{\sum_{i=1}^{nk_1} \min \delta_{ik_2} + \sum_{j=1}^{nk_2} \min \delta_{jk_1}}{2} \quad (2)$$

Here, $\{\min \{\delta\}\}_{\text{rsub}} \{\{ik\}_{\text{rsub}} \{2\}\}$ represents the nearest phylogenetic distance between species “ i ” in community “ k_1 ” and species in community “ k_2 ”, and $\{\min \{\delta\}\}_{\text{rsub}} \{\{jk\}_{\text{rsub}} \{1\}\}$ represents the nearest phylogenetic distance between species “ j ” in community “ k_2 ” and species in community “ k_1 ”.

The net relatedness index (NRI) and the nearest taxon index (NTI) are used to quantify and describe the phylogenetic structures in different communities (Webb, 2000). In general, when the species pool involved in the analysis is large, the combination of the NTI and NRI effectively reflects the assembly mechanism of the community (Kraft et al. 2008). The NRI refers to the standardized effect size of the mean phylogenetic distance (MPD), which measures the mean phylogenetic distance between each of the sampled taxa and every other terminal in the sample. The NTI is related to the mean nearest phylogenetic taxon distance (MNTD), which measures the mean distance between each of the sampled taxa and its own most closely related terminal taxon in the sample (Molina-Venegas et al., 2013). Before calculating the NRI and NTI, it is first assumed that all the species surveyed in the community constitute a local species pool. Keeping the total number of species unchanged, the species in each plot was randomly selected 999 times from the species pool through the random lottery model to obtain the MPD/MNTD distribution of the species in each plot under the random null model. Finally, the random distribution results were used to standardize the observations of MPD/MNTD to obtain the NRI and NTI. The formulas for the calculation of the NRI/NTI are as follows:

$$NRI = -1 \times \frac{(MPD_{\text{observed}} - MPD_{\text{randomized}})}{sd(MPD_{\text{randomized}})} \quad (3)$$

$$NTI = -1 \times \frac{(MNTD_{\text{observed}} - MNTD_{\text{randomized}})}{sd(MNTD_{\text{randomized}})} \quad (4)$$

MPD_{observed} and $MNTD_{\text{observed}}$ are the actual values of the MPD and MNTD, respectively. $MPD_{\text{randomized}}$ and $MNTD_{\text{randomized}}$ are the means of the null model distributions ($n = 999$). $sdMPD_{\text{randomized}}$ and $sdMNTD_{\text{randomized}}$ are the standard deviations of the null model distributions. If $NRI/NTI > 0$, MPD/MNTD is lower than the expected value, indicating phylogenetic structure convergence, and in contrast, $NRI/NTI < 0$ indicates phylogenetic structure overdispersion. The analyses were performed using the picante package in R version 3.5.3 (Kembel et al., 2010).

2.4 Data analysis

313

314 We wanted to understand how the species and phylogenetic α diversity shift along
315 environmental gradients. Hence, a linear regression analysis was performed with the SR, PD, NRI,
316 NTI and elevation gradients. We explicitly modeled the association between diverse environmental
317 factors (e.g., soil, topography, and canopy density) and the community-level α diversity using two
318 multiple stepwise regression models, with one modeling the SR and one modeling the PD. Note that
319 the regression model retained only the environmental variables with statistical significance ($P <$
320 0.05).

321 To explore the mechanisms of changes in species and phylogenetic β diversity among
322 communities, the elevation, soil factor values, and geographic coordinates (latitude and longitude)
323 were standardized, and their Euclidean distances were generated. We used Mantel's test to quantify
324 the correlation between the species and phylogenetic dissimilarity matrix, elevation distance,
325 geographic distance and environmental distance (Zhang et al, 2013). The analyses were performed
326 using the ecodist package in R version 3.6.3. Each Mantel's test generated an r value similar to
327 Pearson's correlation index, which represents the correlation between the distance matrices.
328 Permutation tests were applied to assess the significance of the correlation by randomizing the
329 distance matrix 999 times. We also applied the Vegan package and analyzed the independent
330 interpretations of the elevation distance, environmental distance and geographic distance relative to
331 the β diversity using variance decomposition.

332

333 **3. Results**

334

335 **3.1 Patterns of the variation in the species and phylogenetic α diversity of the *D. pectinatum*** 336 **community at the community and local scales**

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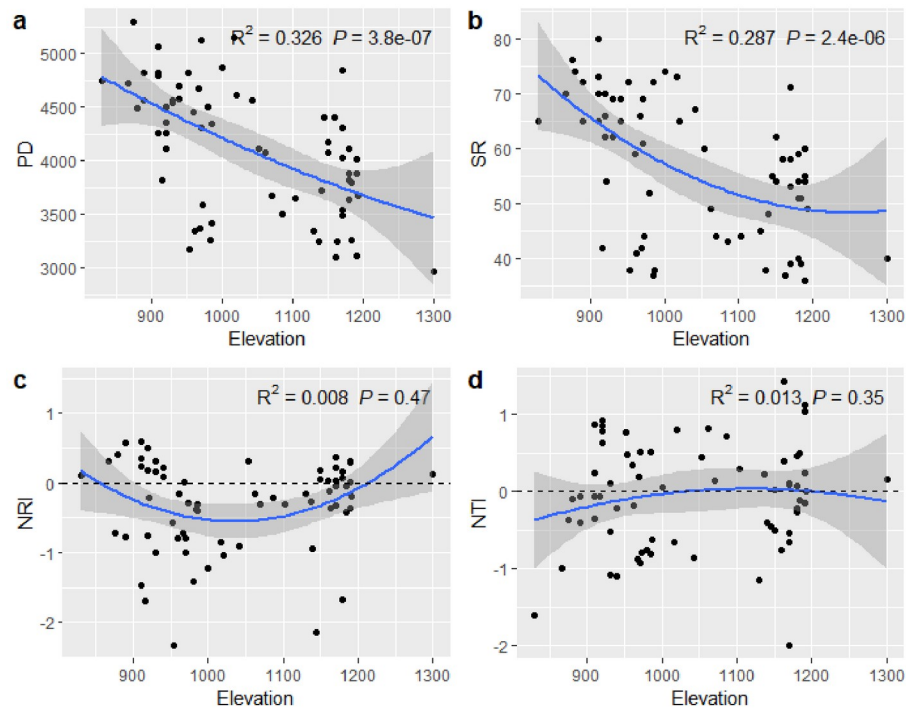


Fig. 3 Elevation patterns of species and phylogenetic α diversity at the community scale. Panel a represents the phylogenetic α diversity (PD); panel b represents the species α diversity (SR); panel c represents the net relatedness index (NRI); and panel d represents the nearest taxon index (NTI). Note that the black dotted lines in panels c and d represent completely random values.

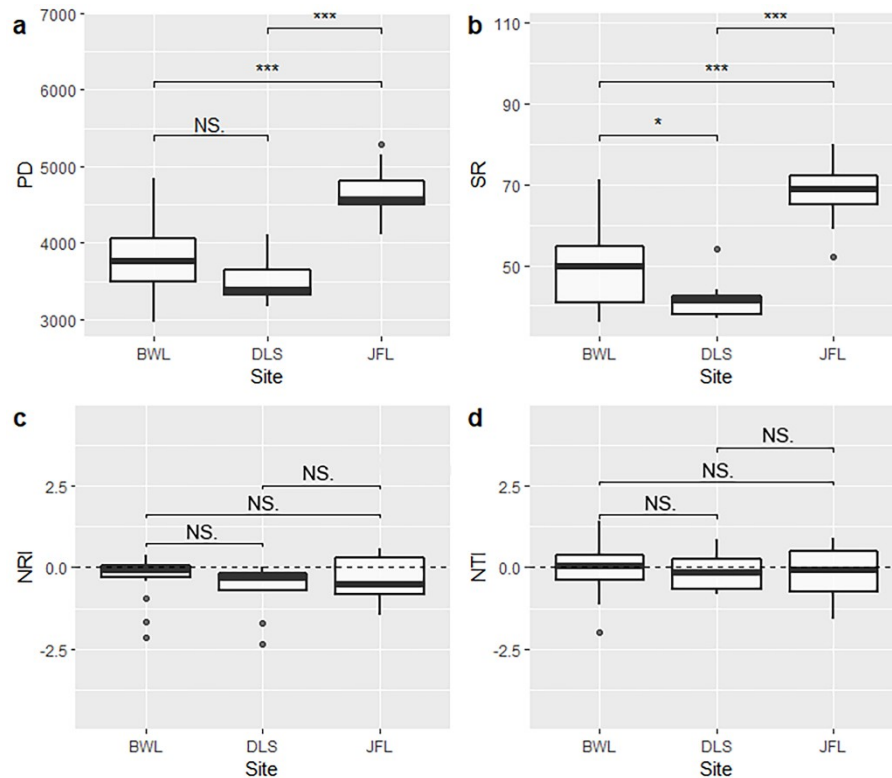


Fig. 4 Changes in species and phylogenetic α diversity at the local scale. BWL represents Bawangling, DLS represents Diaoluoshan, and JFL represents Jianfengling. Panel c represents the phylogenetic α diversity (PD); panel d represents the species α diversity (SR); panel c represents the net relatedness index (NRI); and panel d represents the nearest taxon index (NTI). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and NS represents no significant difference ($P > 0.05$). Note that the black dotted lines in panels c and d represent completely random values.

The community-level species and phylogenetic α diversity presented a consistent elevation pattern, showing a rapid decrease with an increase in elevation, and reached a peak at low elevation ($P < 0.001$) (Fig. 3). However, at the local scale, we found differences in α -diversity patterns. For instance, Jianfengling (elevation between 830 and 1053 m) had the highest species and phylogenetic α diversity and showed significant differences from the other study sites in terms of diversity ($P < 0.001$) (Fig. 4), which were related to the higher species richness of Jianfengling, whereas there were no obvious differences between Bawangling (elevation between 1062 and 1300 m) and Diaoluoshan (elevation between 916 and 986 m). We found that the peaks in species and phylogenetic α diversity frequently occurred between 800 and 1000 m elevations.

The NRI and NTI at the community level demonstrated no obvious pattern with elevation ($P > 0.05$) (Fig. 3). It also did not show significant differences across the three study regions ($P > 0.05$) (Fig. 4). In addition, we found that the two indices of NRI and NTI in most plots were essentially negative values, which shows that the phylogenetic structure of the community exhibits overdispersion patterns.

3.2 Changes in species and phylogenetic β diversity of the *D. pectinatum* community along environmental gradients

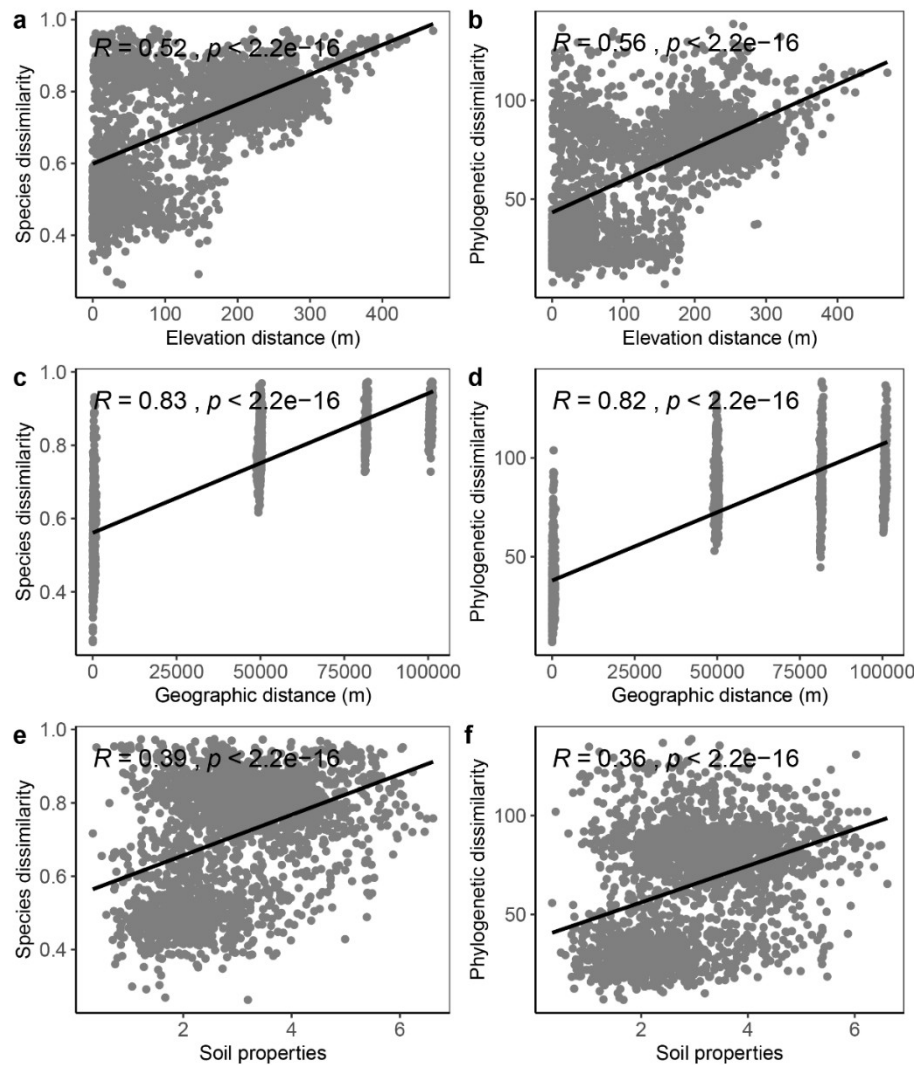
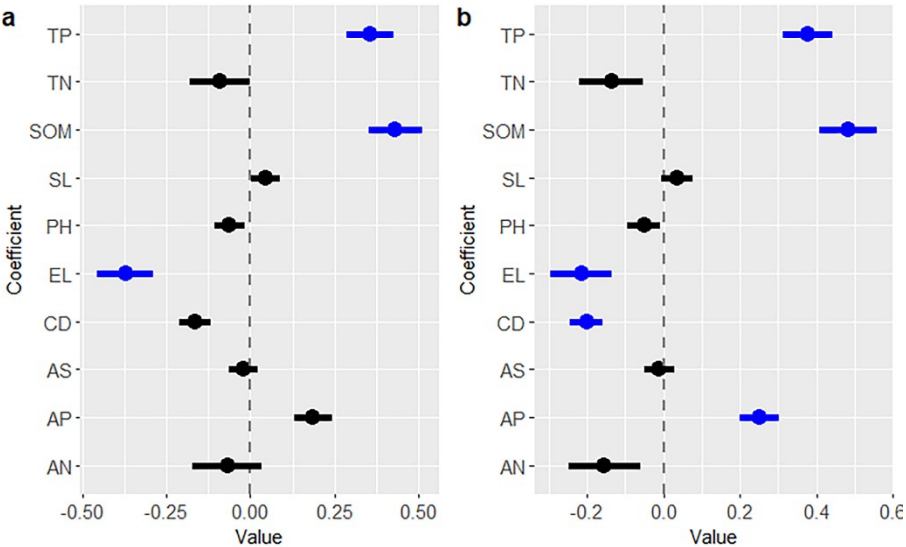


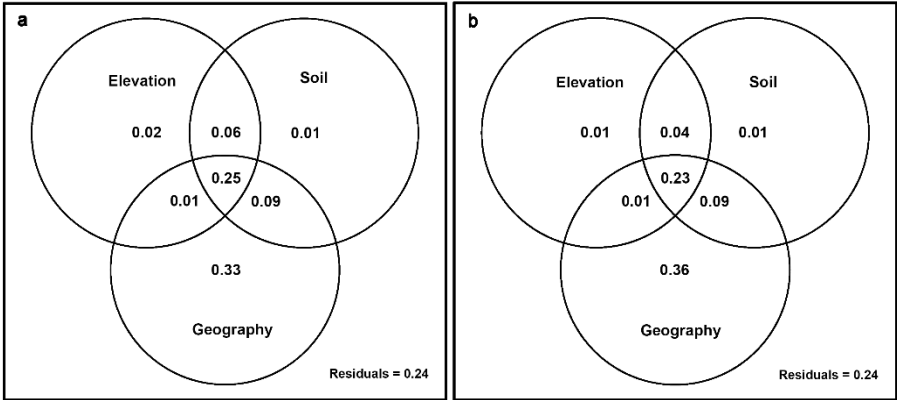
Fig. 5 Species and phylogenetic β diversity shifts with elevation, geographic distance, and soil property differences. Panels a, c, and e illustrate the linear relationships between the species β diversity and elevation and the geographic distance and soil properties, respectively. Panels b, d, and f illustrate the linear relationships between the phylogenetic β diversity and elevation and the geographic distance and soil properties, respectively.

The species and phylogenetic β diversity showed significant positive correlations with the elevation, geographic distance, and soil property differences and presented a consistent increasing pattern (Fig. 5); that is, with an increase in various distances, the difference in the species turnover rate within the community increased. This result indicates that the patterns of changes in species and phylogenetic β diversity may be jointly affected by environmental filtering and dispersal-limiting effects.

384 **3.3 Main factors affecting the species and phylogenetic diversity patterns of the *D. pectinatum***
 385 **community**
 386



387 **Fig. 6** Effects of environmental factors on the community-level species and phylogenetic α
 388 diversity. Panels a and b show the coefficients (with 95% confidence intervals) of the regressions
 389 between various environmental factors and SR and PD, respectively. Blue dots indicate statistical
 390 significance ($P < 0.05$), and black dots indicate no statistical significance ($P > 0.05$). Data for the soil
 391 total phosphorus (TP, $\text{g} \cdot \text{kg}^{-1}$), soil total nitrogen (TN, $\text{g} \cdot \text{kg}^{-1}$), soil organic matter (SOM, $\text{g} \cdot \text{kg}^{-1}$),
 392 slope (SL, $^{\circ}$), soil pH (PH), elevation (EL, m), canopy density (CD, %), aspect (AS), soil available
 393 phosphorus (AP, mg kg^{-1}), and soil available nitrogen (AN, mg kg^{-1}) are provided.
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 395



396 **Fig. 7** Variance in the species and phylogenetic β diversity of the *D. pectinatum* community
 397 explained by elevation, geographical distance, and soil property differences. Panel a represents the
 398 phylogenetic β diversity, and panel b represents the species β diversity.
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We used two multiple stepwise regression models to filter out the most important environmental factors that affect the community-level species and phylogenetic α diversity, and the variance explanation percentages for PD and SR were 58.6% and 62.2%, respectively (Table 2). The PD was significantly correlated with increased TP and SOM and significantly decreased with EL. The SR showed a similar trend, being significantly correlated with increased TP, SOM, and AP but significantly decreasing with increasing EL and CD (Fig. 6).

According to the results of the variance analysis (Fig. 7), geographic distance had the highest explanatory power in terms of the β diversity patterns, and its independent explanatory percentages for the phylogenetic and species β diversity were 32.56% and 36.41%, respectively. The independent interpretation rates of elevation and were only 1.82% and 1.45%, respectively, for elevation and 1.25% and 0.72%, respectively, for soil differences. These results indicate that dispersal limitation affects β -diversity patterns more substantially than does environmental filtering at the spatial scale.

Table 2 Stepwise multiple regression between the community-level species and phylogenetic α diversity and various environmental variables.

Environmental variables	Regression coefficients	Parameters			
		<i>T</i>	<i>P</i>	<i>R</i> ²	<i>AIC</i>
PD				0.586	140.68
Soil organic matter	0.380	2.670	0.000***		
Soil total phosphorus	0.379	2.555	0.000**		
Elevation	-0.446	-2.193	0.003**		
SR				0.622	134.54
Soil organic matter	0.398	3.976	0.000***		
Soil total phosphorus	0.415	4.043	0.000***		
Soil available phosphorus	0.261	2.658	0.010**		
Elevation	-0.336	-2.432	0.018*		
Canopy density	-0.201	-2.459	0.017*		

Note that only the environmental variables with statistical significance were retained in the regression model ($P < 0.05$). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

4. Discussion

4.1 Species and phylogenetic α -diversity patterns of the *D. pectinatum* community change across elevation gradients and at the local scale

In terms of the community-level α -diversity patterns of the *D. pectinatum* community, the patterns were consistent in the species-based and phylogenetic-based analyses in our study. Both presented a monotonically decreasing pattern with elevation, with the peak occurring in the mid-elevation region between 800 and 1000 m. The results of our study confirm previous assumptions. Thorsten et al. (2017) found that species and phylogenetic α diversity were closely related and presented a consistent pattern with elevation. Rahbek (2004) indicated that species distributions might show a moderate expansion phenomenon in mid-elevation regions due to a greater abundance of available resources and the presence of the most suitable hydrothermal conditions. Conversely, some harsh environmental conditions in high-elevation regions, such as low temperatures, reduced precipitation, a high frequency of fog, and scarce soil nutrients, will cause species at low elevations to be filtered as they migrate to higher elevations (Guevara, 2005). In addition, the patterns of the changes in α diversity at the local scale also indirectly validated the environmental filtering hypothesis; for instance, Jianfengling in mid-elevation areas was significantly more diverse than Bawangling and Diaoluoshan due to the more suitable hydrothermal conditions. This evidence indicates that environmental filtering plays an important role in the formation of species and phylogenetic α diversity. We also found that although Jianfengling and Diaoluoshan had similar habitat conditions, they had different diversity patterns. We believe that this difference might be explained by the time-species formation hypothesis (Lomolino, 2001) because regions with earlier colonization histories generally tend to have higher diversities (note Jianfengling and Diaoluoshan nature reserves were established in 1960 and 1984, respectively).

The phylogenetic structure of a plant community can reveal the ecological process of diversity distribution (Kembel and Hubbell, 2006). The phylogenetic structure of the *D. pectinatum* community essentially showed an overdispersion pattern along the elevation gradients, but a convergence pattern appeared in some relatively high-elevation plots. A previous study indicated that the phylogenetic structure of a tropical rainforest community in Malaysia presented an overdispersion pattern at low elevations, shifting to a convergence distribution pattern at high elevations (Webb, 2000). Huang et al. (2010) found a similar pattern in a subtropical evergreen broad-leaved forest. Based on the differences across the three study sites, we found that Diaoluoshan and Jianfengling both showed phylogenetic overdispersion patterns at low-middle elevations, while in some plots at Bawangling with higher elevations, a convergence distribution was observed. Hence, environmental filtering might cause the phylogenetic structure of the

community to tend to converge in relatively high-elevation regions, which in turn affects the assembly patterns of the plant community (Kitching, 2013; Souza-Neto et al, 2015). However, in low- and mid-elevation regions, community assembly is mainly affected by various factors, such as environmental filtering, similarity restrictions, and anthropogenic disturbance (Kraft et al, 2008). For example, Ding et al. (2011) suggested that in tropical forest habitats with high species richness and some degree of disturbance, phylogenetic structures are most likely to show an overdispersed pattern.

Changes in elevation across a relatively short geographic distance result in large environmental changes in such factors as climate, geometric constraints (e.g., boundary constraints) and anthropogenic activity intensity (Parks et al., 2005; Zhang et al, 2015). Hence, elevation usually indirectly affects the assembly patterns of plant communities by changing other environmental factors (Rahbek, 2004; Dainese et al, 2015). The species and phylogenetic α diversity showed a significant positive correlation with the SOM, TP and AP and a negative correlation with the canopy density in this study. Organic matter contains nutrients necessary for plant growth, and its absence will lead to a reduction in the number of species, which in turn will cause a decline in the species diversity (Fornara et al, 2009). Previous studies have found that phosphorus in tropical forest soils is generally lacking (note that the total phosphorus content is mostly below $0.8 \text{ g}\cdot\text{kg}^{-1}$) (Cleveland et al., 2011). Phosphorus is a key indicator of photosynthesis in plants, and a lack of this nutrient will affect diversity distribution patterns (Long et al, 2011). The canopy density directly affects the ability of the vegetation under the canopy to obtain light, which in turn affects the natural regeneration of the community (Gao et al, 2017). Many reports have indicated that light is the main source of energy required for the growth of tree seedlings and saplings, and thus, the canopy density usually plays an important role in the coexistence of species in tropical forests (Jiang et al, 2015).

4.2 Changes in the species and phylogenetic β -diversity patterns of the *D. pectinatum* community along environmental gradients

β diversity is generally used to assess the mechanisms of community assembly in heterogeneous spaces by exploring changes in species compositions, phylogenetic structures, and functional traits among communities (Cardoso et al, 2014). In general, the greater are the differences in species similarity, phylogenetic relationships and trait combinations along environmental gradients, the higher is the β diversity among communities (Legendre, 2007). In this study, the species and phylogenetic β diversity of the *D. pectinatum* community showed consistent positive correlations with the elevation, geographical distance, and soil property differences. In

addition, with changes in various distances, the differences in species composition between communities increased, which indicates that environmental filtering and dispersal restrictions affect the turnover of plants in the community. Under the assumption of the Rapoport hypothesis, plants occupy little space and resources in tropical forests, usually exhibiting environmental specificity, and show a high species turnover rate, even at the spatial scale with the fewest changes (Simberloff et al, 1983). Previous studies have suggested that both deterministic and stochastic processes play a role in plant community assembly in tropical and subtropical environments and that the coexistence and maintenance of species are the result of random drift and niche differentiation (Muoz et al, 2016). For example, Lu et al. (2013) found that species β diversity is significantly affected by distance and topography and that its correlations with geographic distance and topographic differences show similar monotonous increasing trends with increasing differences. Zhang et al. (2012) also revealed similar results, showing that changes in phylogenetic β diversity are related to geographic distance and environmental differences and that the phylogenetic structure changes from overdispersion to convergence with increasing spatial scales.

However, the relative contributions of deterministic and stochastic processes to community assembly patterns at the spatial scale—that is, the identification of which factors play key roles—remain controversial. One view is that the main factors affecting the species compositions of communities are two opposite processes, habitat filtering and similarity limitation (Webb et al, 2002), and another is that the differences in composition between communities are related only to geographic distance and not to other environmental factors as the spatial scale increases (Chase and Myers, 2011). In fact, the relative importance of these processes varies across different habitats and scales. For example, in grassland communities, the community structure is relatively simple, and niche differentiation thus plays a major role, while in species-rich tropical forests, the maintenance of species diversity is mainly dominated by neutral processes (Gravel et al, 2006). Based on the variance results, geographic distance has the highest explanatory power in terms of β diversity, while differences in elevation and soil properties explain only minor changes, which indicates that dispersal restriction plays a more key role compared to niche differentiation in driving the assembly of tropical plant communities in a heterogeneous space with complex habitats.

5. Conclusion

This study indicates that the species and phylogenetic α -diversity patterns of the *D. pectinatum* community present a consistent decreasing pattern with elevation, with the peak occurring at low elevation. Environmental filtering caused by decreases in some limiting factors, such as the

524 temperature, precipitation, soil organic matter, soil phosphorus, and light, is the main reason for the
525 decline in diversity in high-elevation areas, whereas low-elevation areas are affected by various
526 factors, such as environmental filtering and similarity limitation. Changes in species and
527 phylogenetic β diversity are closely related to environmental filtering and dispersal limitation, but
528 the latter plays a key role in community assembly at a heterogeneous spatial scale. In addition, the
529 time-species formation hypothesis provides important guidance for exploring diversity patterns in
530 diverse areas. In conclusion, combining species-based and phylogenetic-based methods to explore
531 the biogeographic patterns of tropical plant communities helps provide important data and confirms
532 that the relative contributions of niche and neutral theory in the assembly process vary across
533 environmental gradients. Though the species in the *D. pectinatum* community constitute a
534 floristically integrated unit, the genetic relationship between the species is relatively far, and it is
535 difficult for the community to co-evolve to promote species coexistence when faced with habitat
536 pressure. Hence, we believe that the species coexistence in tropical plant communities requires mild
537 environmental conditions, and the effects of habitat pressure will aggravate environmental filtering
538 and species competition.

539

540 **Data availability statement**

541

542 All authors agreed to deposit data from this manuscript to a public repository. Data are submitted to
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544

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557

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783 **Appendix S1**

784
785 **Table S1** Summary of the plant species composition and stand characteristics of the *D. pectinatum*
786 community.

Site	No. of families	No. of genera	No. of species	No. of stems	DBH	H	N
BWL	52	101	187	5386	14.51±1.34 ^a	10.41±0.74 ^a	1994.43±511.65 ^b

DLS	41	73	126	1023	14.35±8.68 ^a	10.44±1.29 ^a	1700.93±409.84 ^a
JFL	54	110	186	5705	15.15±1.11 ^b	10.73±1.39 ^b	2112.59±357.39 ^c

Species data are based on tree abundance data from sixty-eight permanent plots in *D. pectinatum* communities. BWL represents Bawangling, DLS represents Diaoluoshan, and JFL represents Jianfengling. The mean diameter at breast height of the stand (DBH, cm), mean height of the stand (H, m), and density of the stand (N, stems/hm²) are expressed as the mean \pm sd.

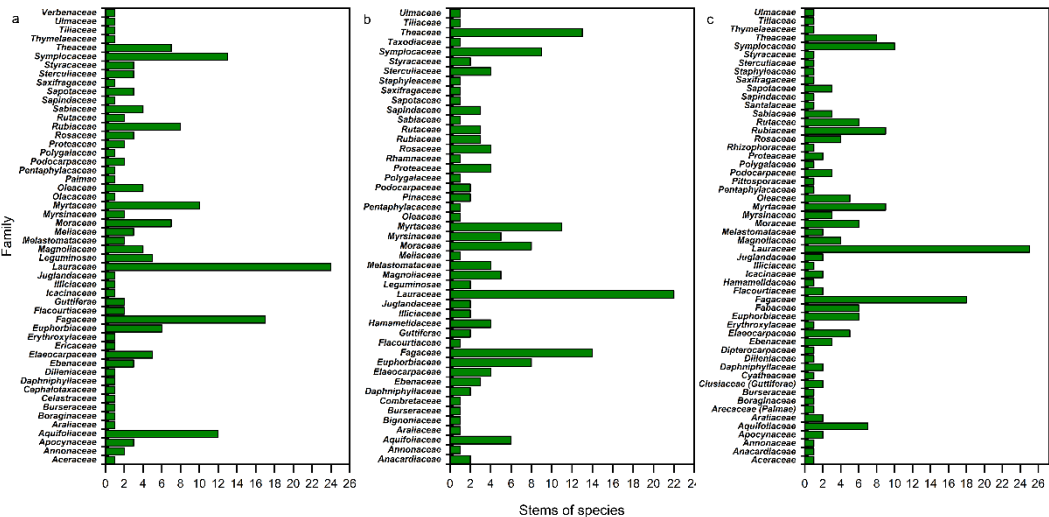
Table S2 Dominance of 30 species selected using calculated importance values (IV = Relative frequency + Relative density + Relative dominance) across the three *D. pectinatum* communities.

Species	Family	IV	N	H	H _{max}	DBH	D _{max}	BA
Bawangling								
<i>Dacrydium pectinatum</i>	<i>Podocarpaceae</i>	8.68	34	18.2	30.0	59.5	194.0	13.78
<i>Castanopsis carlesii</i>	<i>Fagaceae</i>	4.94	127	12.6	22.6	17.4	68.8	4.05
<i>Syzygium araiocladum</i>	<i>Myrtaceae</i>	4.89	167	9.8	20.8	12.5	33.7	2.49
<i>Cryptocarya chinensis</i>	<i>Lauraceae</i>	3.27	129	7.8	17.0	9.5	31.1	1.16
<i>Illicium ternstroemioides</i>	<i>Magnoliaceae</i>	3.01	111	8.0	18.1	9.4	27.4	0.88
<i>Xanthophyllum hainanense</i>	<i>Polygalaceae</i>	2.70	59	11.9	21.2	16.8	53.0	1.82
<i>Ilex kobuskiana</i>	<i>Aquifoliaceae</i>	1.95	56	9.8	19.0	11.6	29.3	0.72
<i>Syzygium championii</i>	<i>Myrtaceae</i>	1.80	49	9.3	20.0	11.0	88.0	0.75
<i>Symplocos adenophylla</i>	<i>Symplocaceae</i>	1.49	47	9.1	19.7	8.6	14.5	0.30
<i>Lindera robusta</i>	<i>Lauraceae</i>	1.44	41	11.1	17.0	12.2	36.9	0.59
Diaoluoshan								
<i>Dacrydium pectinatum</i>	<i>Podocarpaceae</i>	15.86	124	11.2	21.0	30.5	130.5	12.33
<i>Cyclobalanopsis champinonii</i>	<i>Fagaceae</i>	4.74	43	11.2	17.6	30.6	78.7	3.17
<i>Altingia chinensis</i>	<i>Hamamelidaceae</i>	3.00	39	11.3	18.0	22.2	50.7	1.51
<i>Adinandra hainanensis</i>	<i>Theaceae</i>	2.65	42	10.0	15.7	16.8	38.9	0.89
<i>Michelia shiluensis</i>	<i>Magnoliaceae</i>	2.59	46	10.0	16.4	15.9	39.5	0.83
<i>Castanopsis carlesii</i>	<i>Fagaceae</i>	2.54	42	9.6	15.6	18.2	38.2	0.98
<i>Xanthophyllum hainanense</i>	<i>Polygalaceae</i>	2.44	39	10.4	14.8	17.4	47.4	0.85
<i>Castanopsis jianfenglingensis</i>	<i>Fagaceae</i>	2.21	39	9.1	14.6	16.7	48.9	0.82
<i>Alstonia scholaris</i>	<i>Apocynaceae</i>	1.93	36	9.0	13.3	12.1	35.8	0.39
<i>Daphniphyllum paxianum</i>	<i>Daphniphyllaceae</i>	1.85	38	9.3	14.5	11.9	30.4	0.38
Jianfengling								

<i>Gironniera subaequalis</i>	<i>Ulmaceae</i>	4.55	130	10.8	25.0	15.6	41.0	3.03
<i>Livistona saribus</i>	<i>Palmae</i>	4.48	67	8.9	28.0	31.2	50.0	5.28
<i>Dacrydium pectinatum</i>	<i>Podocarpaceae</i>	4.26	17	21.1	36.0	62.9	105.2	6.00
<i>Cryptocarya chinensis</i>	<i>Lauraceae</i>	3.74	123	10.2	30.0	11.7	35.8	1.70
<i>Alseodaphne hainanensis</i>	<i>Lauraceae</i>	3.00	69	10.8	25.0	17.1	55.8	2.23
<i>Beilschmiedia tungfangensis</i>	<i>Lauraceae</i>	2.35	64	10.6	30.0	12.1	43.5	1.13
<i>Cryptocarya chingii</i>	<i>Lauraceae</i>	2.06	63	9.7	22.0	10.1	25.9	0.60
<i>Nephelium topengii</i>	<i>Sapindaceae</i>	1.86	54	9.9	26.0	10.4	33.9	0.62
<i>Psychotria rubra</i>	<i>Rubiaceae</i>	1.60	49	5.6	11.0	7.1	13.7	0.21
<i>Cinnamomum burmanni</i>	<i>Lauraceae</i>	1.57	43	9.4	38.0	9.7	27.5	0.40

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796

797 **Fig. S3** The abundance distribution of plant families in *D. pectinatum* communities. Panel a

798 provides data for Bawangling, panel b provides data for Diaoluoshan, and panel c provides data for

799 Jianfengling.