

# 1 Identifying the patterns of changes in $\alpha$ and $\beta$ diversity across 2 *Dacrydium pectinatum* communities in Hainan Island, China

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4 Haodong Liu,<sup>1,2</sup> Hua Liu,<sup>1,2</sup> Yongfu Chen,<sup>1,2</sup> Zhiyang Xu,<sup>2,3</sup> Yunchuan Dai,<sup>4</sup> Qiao Chen<sup>1,2,\*</sup>

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6 <sup>1</sup> Research Institute of Forest Resource Information Techniques, Chinese Academy of Forestry,  
7 Beijing, 100091, China.

8 <sup>2</sup> Key Laboratory of Forest Management and Growth Modelling, NFGA.

9 <sup>3</sup> East China Inventory and Planning Institute of National Forestry and Grassland Administration,  
10 Hangzhou, 321000, Zhejiang, China.

11 <sup>4</sup> Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry,  
12 Beijing, 100091, China.

13

14 Email: [chengqiqo@163.com](mailto:chengqiqo@163.com).

15

## 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  $\alpha$ - and  $\beta$ -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  $\alpha$ -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  $\beta$ -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

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

43

44 **Keywords** Biodiversity hotspots, *Dacrydium pectinatum*, deterministic processes, stochastic  
45 processes,  $\alpha$  and  $\beta$  diversity, Hainan Island

46

## 47 **1. Introduction**

48

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

64 Strong evidence indicates the existence of both significant variation and a large degree of  
65 overlap in microhabitat preferences among species in diverse subtropical and tropical forests (Kraft  
66 et al., 2008, Lai et al., 2009), and species with similar microhabitat requirements often spatially  
67 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  $\beta$  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

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

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

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

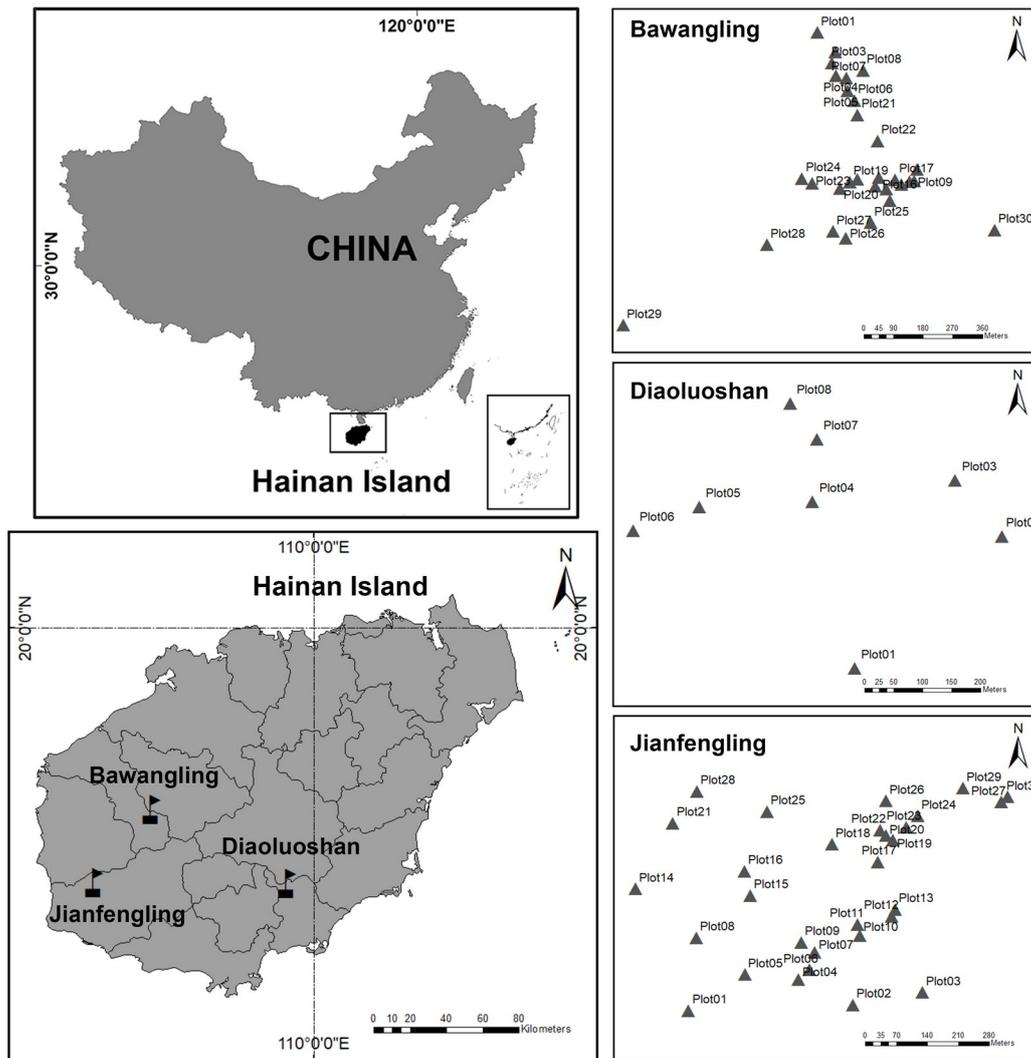
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## 132 **2. Materials and methods**

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### 134 **2.1 Study sites**

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136  
 137 **Fig. 1** Permanent plot locations in the natural *D. pectinatum* communities in the three national  
 138 nature reserves of Bawangling, Diaoluoshan and Jianfengling, Hainan Island, China.

139

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

146 *Dacrydium pectinatum* is one of the constructive and endangered species in the tropical  
 147 mountain forests of Hainan Island and belongs to the *Podocarpaceae* family (Keppel et al., 2011).  
 148 Its modern distribution in the Northern Hemisphere is limited to approximately 20°N south, and it  
 149 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 hm<sup>2</sup>, 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 hm<sup>2</sup>, 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 km<sup>2</sup>, 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).

184 The detailed coordinate, climate and topography data for the three study sites are shown in  
 185 Table 1 (elevation data from field records). The climate data, including the annual mean  
 186 temperature and the annual precipitation, were extracted from the information on the current  
 187 conditions (1950–2000) in the WorldClim global climate database (<http://www.worldclim/>).  
 188

189 **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 <sup>b</sup>	20.74±1.78 <sup>a</sup>	1617.76±116.52 <sup>b</sup>
DLS					
TMRF	18°43'N	109°43'E	935.97±22.96 <sup>a</sup>	21.89±1.60 <sup>b</sup>	1806.73±98.13 <sup>c</sup>
JFL					
TMRF	18°20'N	108°41'E	907.43±46.54 <sup>a</sup>	21.75±1.52 <sup>b</sup>	1520.33±135.14 <sup>a</sup>

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

## 194 2.2 Field investigation and plant sampling

195  
 196 Field investigations were conducted from December 2017 to July 2018. Because endangered  
 197 species mostly occur in low-density populations with small quantities and scattered distributions,  
 198 the minimum-area sampling method was more suitable for this study compared to the large-scale  
 199 survey method. We established sixty-eight permanent plots across Bawangling, Diaoluoshan, and  
 200 Jianfengling. Based on previous surveys and the experience of local forestry workers, we  
 201 constructed the plots under the following considerations: (1) the plots must contain varying  
 202 numbers of adult *D. pectinatum* individuals, and *D. pectinatum* must be a top-level plant species;  
 203 (2) the conditions within the stand must be relatively uniform and show limited human interference;  
 204 and (3) if the sites meets the above criteria, the plot is randomly established within the stand. We  
 205 established 30 plots in Bawangling and 30 plots in Jianfengling, each of which had an area of 900  
 206 m<sup>2</sup> (30×30 m). Due to the severe deforestation in Diaoluoshan, we established only 8 permanent  
 207 plots at this location.

208 All woody stems (including those of trees, shrubs, and lianas) with a diameter at breast height  
 209 (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 m<sup>2</sup> (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<sup>-1</sup>, potassium dichromate oxidation  
234 volumetric method, LY/T 1237-1999), soil total nitrogen (TN, g·kg<sup>-1</sup>, Kjeldahl boiling-diffusion  
235 method, LY/T 1228-1999), soil total phosphorus (TP, g·kg<sup>-1</sup>, sodium hydroxide alkaline fusion-  
236 molybdenum anti-colorimetric method, LY/T 1232-1999), soil alkaline nitrogen (AN, mg·kg<sup>-1</sup>,  
237 alkaline hydrolysis- diffusion method, LY/T 1229-1999), soil available phosphorus (AP, mg·kg<sup>-1</sup>,  
238 0.05 mol·L<sup>-1</sup> HCl-0.025 mol·L<sup>-1</sup> 1/2 H<sub>2</sub>SO<sub>4</sub> extraction method, LY/T 1233-1999), and soil pH (pH,  
239 H<sub>2</sub>O 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 $\alpha$ and $\beta$ diversity**

247

248 In this study, we used the species richness index (SR) as a measure of the species  $\alpha$  diversity,  
249 which represents the number of species in each plot. To analyze the patterns of the species  $\beta$   
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):

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

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.

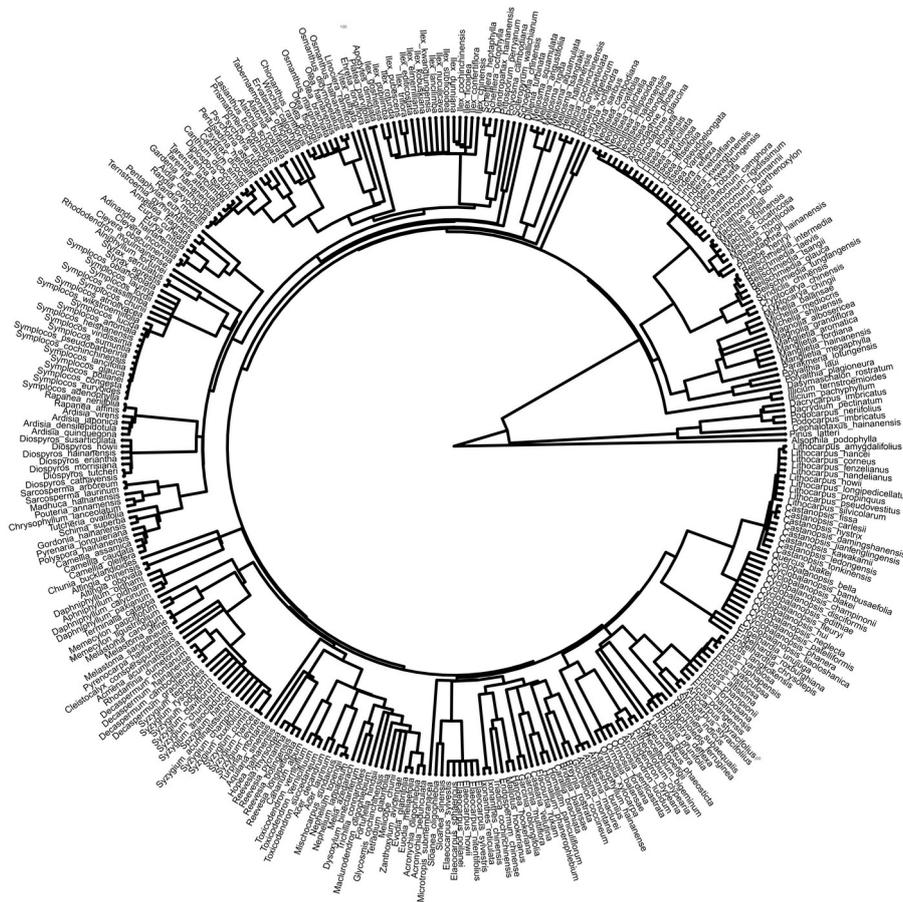
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### 257 **2.4.2 Phylogenetic tree construction**

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



267  
 268 **Fig. 2.** Phylogenetic tree of *D. pectinatum* communities constructed using the V.PhyloMaker  
 269 including 344 taxa distributed across 150 genera in 69 families.

270

### 271 **2.4.3 Phylogenetic $\alpha$ and $\beta$ diversity**

272

273 The statistical analyses and data processing were mainly carried out in R statistical software  
 274 3.6.3. Faith's PD (PD) was used as a measure to describe the phylogenetic  $\alpha$  diversity, and this  
 275 value is the sum of the minimum spanning path in the phylogenetic tree connecting all species  
 276 found in a local plot (Faith, 1992). In recent years, various phylogenetic  $\beta$  diversity measures have  
 277 been proposed, such as the mean phylogenetic dissimilarity ( $D_{pw}$ ) between the individuals or species  
 278 in two communities (Rao, 1982; Webb et al., 2008), the mean nearest taxon distance ( $D_{nn}$ ) between  
 279 the individuals or species in two communities (Webb et al., 2002; Webb et al., 2008), and the  
 280 amount of phylogenetic branch length shared between species in two communities (PhyloSor,  
 281 Bryant et al., 2008). We used the mean nearest taxon distance ( $D_{nn}$ ) to assess the phylogenetic  $\beta$   
 282 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*<sub>1</sub>” and species in community “*k*<sub>2</sub>”, and  $\{\min \{\delta\}\}_{\text{rsub}\{\{jk\}_{\text{rsub}\{1\}\}}$  represents the nearest phylogenetic distance between species “*j*” in community “*k*<sub>2</sub>” and species in community “*k*<sub>1</sub>”.

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:

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

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

$MPD_{\text{observed}}$  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).

311

## 312 2.4 Data analysis

313

314 We wanted to understand how the species and phylogenetic  $\alpha$  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  $\alpha$  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  $\beta$  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  $\beta$  diversity using variance decomposition.

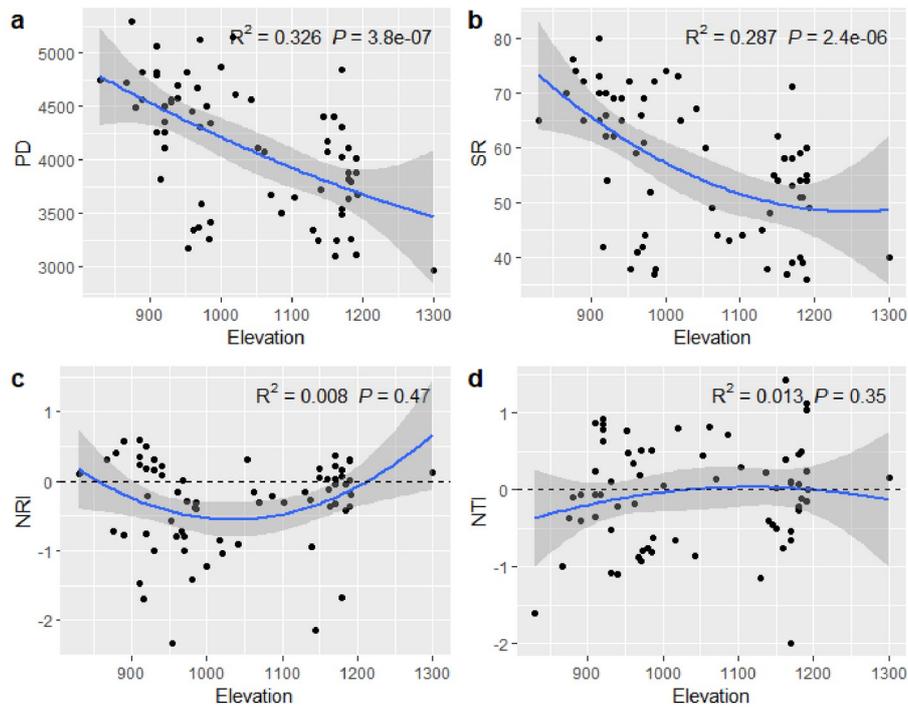
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### 333 **3. Results**

334

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

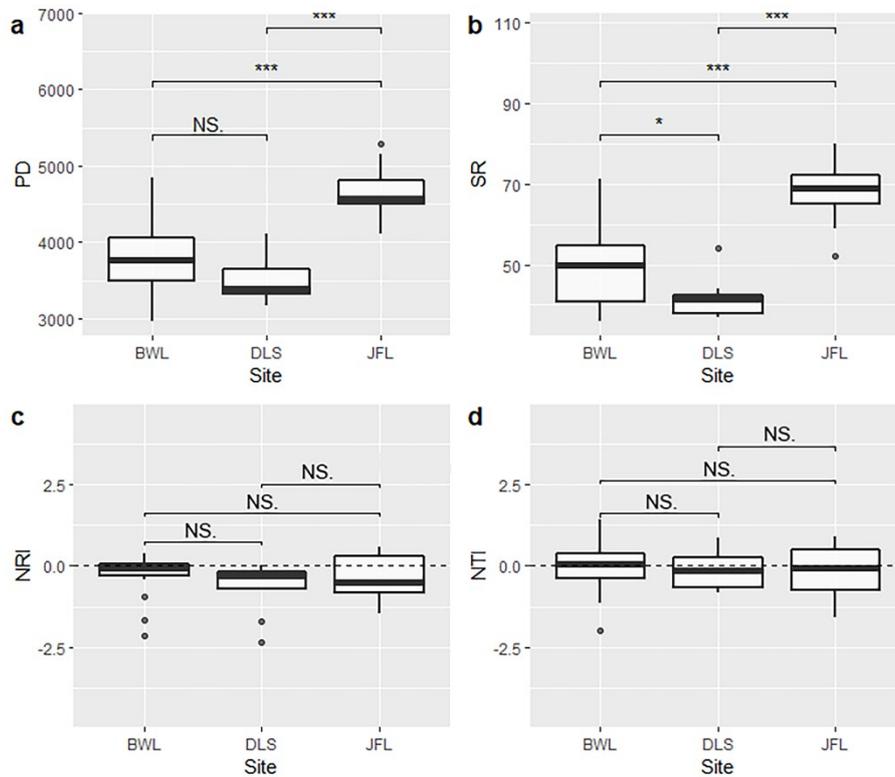
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338

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

343



344

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

351

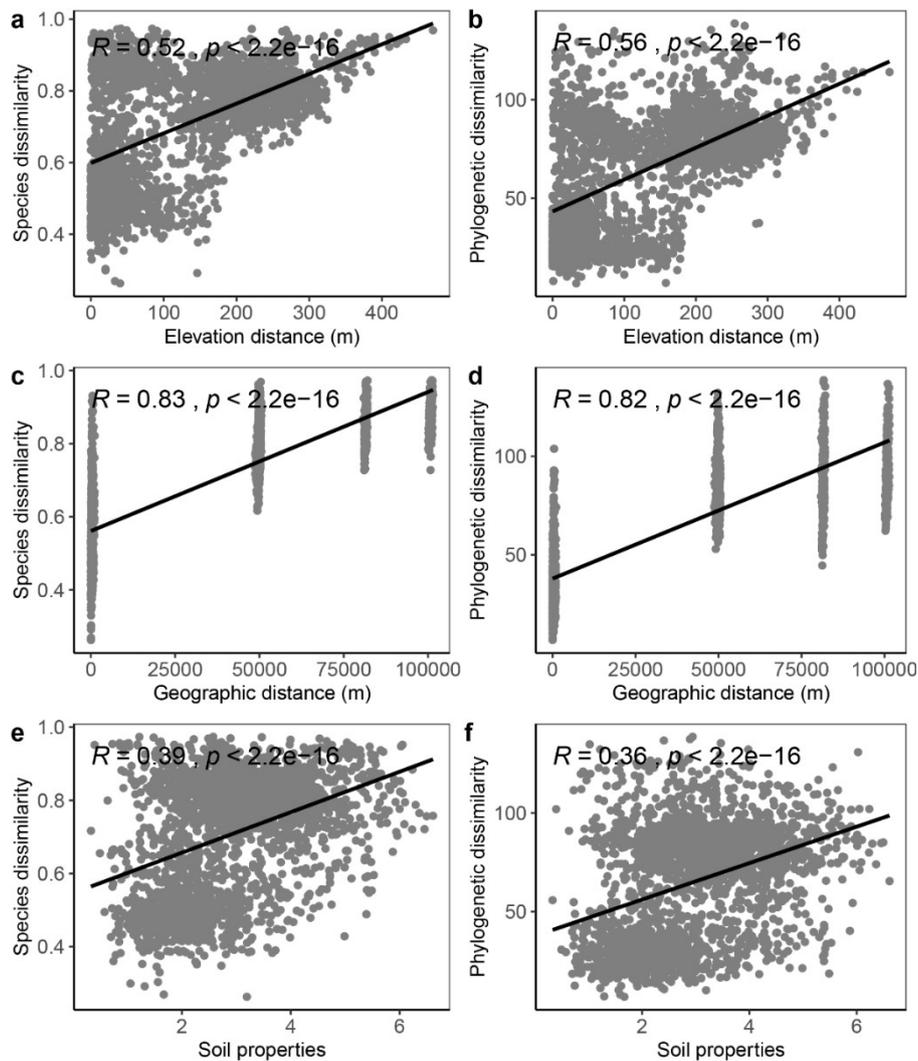
352 The community-level species and phylogenetic  $\alpha$  diversity presented a consistent elevation  
353 pattern, showing a rapid decrease with an increase in elevation, and reached a peak at low elevation  
354 ( $P < 0.001$ ) (Fig. 3). However, at the local scale, we found differences in  $\alpha$ -diversity patterns. For  
355 instance, Jianfengling (elevation between 830 and 1053 m) had the highest species and phylogenetic  
356  $\alpha$  diversity and showed significant differences from the other study sites in terms of diversity ( $P <$   
357  $0.001$ ) (Fig. 4), which were related to the higher species richness of Jianfengling, whereas there  
358 were no obvious differences between Bawangling (elevation between 1062 and 1300 m) and  
359 Diaoluoshan (elevation between 916 and 986 m). We found that the peaks in species and  
360 phylogenetic  $\alpha$  diversity frequently occurred between 800 and 1000 m elevations.

361 The NRI and NTI at the community level demonstrated no obvious pattern with elevation ( $P >$   
362  $0.05$ ) (Fig. 3). It also did not show significant differences across the three study regions ( $P > 0.05$ )  
363 (Fig. 4). In addition, we found that the two indices of NRI and NTI in most plots were essentially  
364 negative values, which shows that the phylogenetic structure of the community exhibits  
365 overdispersion patterns.

366

### 367 **3.2 Changes in species and phylogenetic $\beta$ diversity of the *D. pectinatum* community along** 368 **environmental gradients**

369



370

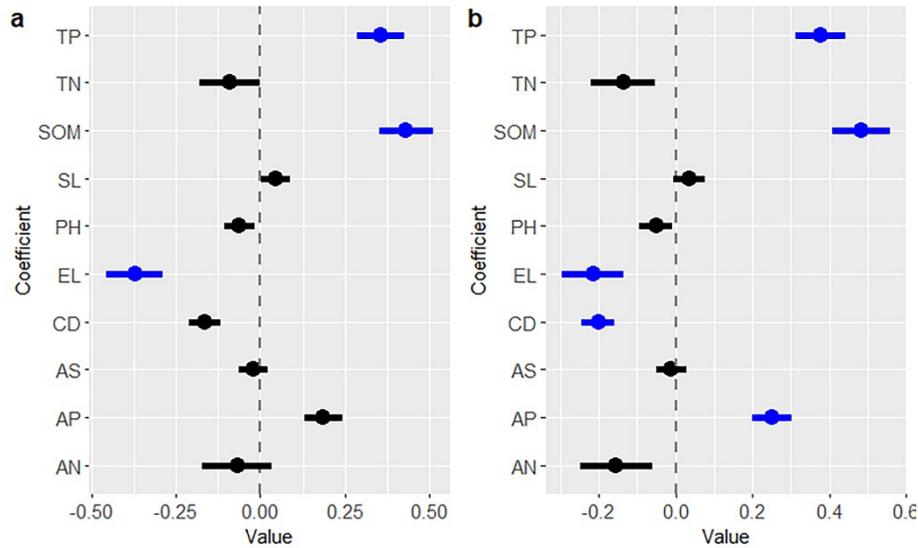
371 **Fig. 5** Species and phylogenetic  $\beta$  diversity shifts with elevation, geographic distance, and soil  
 372 property differences. Panels a, c, and e illustrate the linear relationships between the species  $\beta$   
 373 diversity and elevation and the geographic distance and soil properties, respectively. Panels b, d,  
 374 and f illustrate the linear relationships between the phylogenetic  $\beta$  diversity and elevation and the  
 375 geographic distance and soil properties, respectively.

376

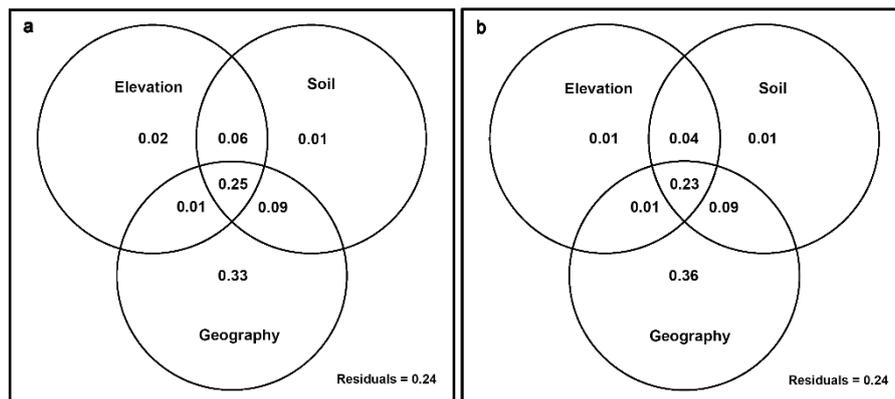
377 The species and phylogenetic  $\beta$  diversity showed significant positive correlations with the  
 378 elevation, geographic distance, and soil property differences and presented a consistent increasing  
 379 pattern (Fig. 5); that is, with an increase in various distances, the difference in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

383

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



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



396  
 397 **Fig. 7** Variance in the species and phylogenetic  $\beta$  diversity of the *D. pectinatum* community  
 398 explained by elevation, geographical distance, and soil property differences. Panel a represents the  
 399 phylogenetic  $\beta$  diversity, and panel b represents the species  $\beta$  diversity.  
 400

401 We used two multiple stepwise regression models to filter out the most important  
 402 environmental factors that affect the community-level species and phylogenetic  $\alpha$  diversity, and the  
 403 variance explanation percentages for PD and SR were 58.6% and 62.2%, respectively (Table 2).  
 404 The PD was significantly correlated with increased TP and SOM and significantly decreased with  
 405 EL. The SR showed a similar trend, being significantly correlated with increased TP, SOM, and AP  
 406 but significantly decreasing with increasing EL and CD (Fig. 6).

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

414

415 **Table 2** Stepwise multiple regression between the community-level species and phylogenetic  $\alpha$   
 416 diversity and various environmental variables.

Environmental variables	Regression coefficients	Parameters			
		<i>T</i>	<i>P</i>	<i>R</i> <sup>2</sup>	<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*		

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

419

#### 420 4. Discussion

421

#### 422 **4.1 Species and phylogenetic $\alpha$ -diversity patterns of the *D. pectinatum* community change** 423 **across elevation gradients and at the local scale**

424

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

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

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

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

479

#### 480 **4.2 Changes in the species and phylogenetic $\beta$ -diversity patterns of the *D. pectinatum*** 481 **community along environmental gradients**

482

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

490 addition, with changes in various distances, the differences in species composition between  
491 communities increased, which indicates that environmental filtering and dispersal restrictions affect  
492 the turnover of plants in the community. Under the assumption of the Rapoport hypothesis, plants  
493 occupy little space and resources in tropical forests, usually exhibiting environmental specificity,  
494 and show a high species turnover rate, even at the spatial scale with the fewest changes (Simberloff  
495 et al, 1983). Previous studies have suggested that both deterministic and stochastic processes play a  
496 role in plant community assembly in tropical and subtropical environments and that the coexistence  
497 and maintenance of species are the result of random drift and niche differentiation (Muoz et al,  
498 2016). For example, Lu et al. (2013) found that species  $\beta$  diversity is significantly affected by  
499 distance and topography and that its correlations with geographic distance and topographic  
500 differences show similar monotonous increasing trends with increasing differences. Zhang et al.  
501 (2012) also revealed similar results, showing that changes in phylogenetic  $\beta$  diversity are related to  
502 geographic distance and environmental differences and that the phylogenetic structure changes from  
503 overdispersion to convergence with increasing spatial scales.

504 However, the relative contributions of deterministic and stochastic processes to community  
505 assembly patterns at the spatial scale—that is, the identification of which factors play key roles—  
506 remain controversial. One view is that the main factors affecting the species compositions of  
507 communities are two opposite processes, habitat filtering and similarity limitation (Webb et al,  
508 2002), and another is that the differences in composition between communities are related only to  
509 geographic distance and not to other environmental factors as the spatial scale increases (Chase and  
510 Myers, 2011). In fact, the relative importance of these processes varies across different habitats and  
511 scales. For example, in grassland communities, the community structure is relatively simple, and  
512 niche differentiation thus plays a major role, while in species-rich tropical forests, the maintenance  
513 of species diversity is mainly dominated by neutral processes (Gravel et al, 2006). Based on the  
514 variance results, geographic distance has the highest explanatory power in terms of  $\beta$  diversity,  
515 while differences in elevation and soil properties explain only minor changes, which indicates that  
516 dispersal restriction plays a more key role compared to niche differentiation in driving the assembly  
517 of tropical plant communities in a heterogeneous space with complex habitats.

518

## 519 **5. Conclusion**

520

521 This study indicates that the species and phylogenetic  $\alpha$ -diversity patterns of the *D. pectinatum*  
522 community present a consistent decreasing pattern with elevation, with the peak occurring at low  
523 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  $\beta$  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  
543 Dryad, and DOI number is <https://doi.org/10.5061/dryad.pc866t1mj>.

544

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550

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553

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555 partly or entirely published in or submitted to any other journals. All of the authors agree to the  
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557

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782  
783 **Appendix S1**

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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 <sup>a</sup>	10.41±0.74 <sup>a</sup>	1994.43±511.65 <sup>b</sup>

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

787 Species data are based on tree abundance data from sixty-eight permanent plots in *D. pectinatum*  
788 communities. BWL represents Bawangling, DLS represents Diaoluoshan, and JFL represents  
789 Jianfengling. The mean diameter at breast height of the stand (DBH, cm), mean height of the stand  
790 (H, m), and density of the stand (N, stems/hm<sup>2</sup>) are expressed as the mean ± sd.

791

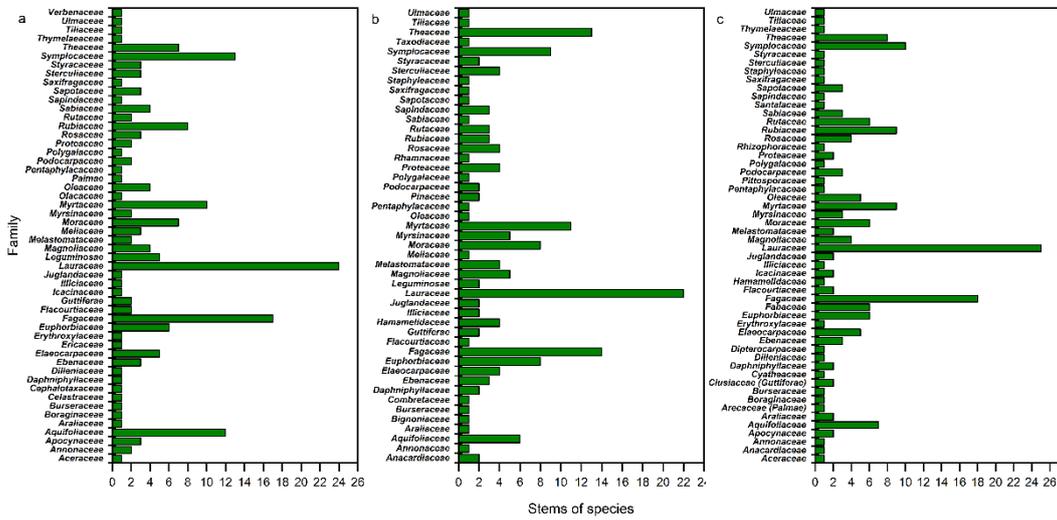
792 **Table S2** Dominance of 30 species selected using calculated importance values (IV = Relative  
793 frequency + Relative density + Relative dominance) across the three *D. pectinatum* communities.

Species	Family	IV	N	H	H <sub>max</sub>	DBH	D <sub>max</sub>	BA
<b>Bawangling</b>								
<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
<b>Diaoluoshan</b>								
<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
<b>Jianfengling</b>								

<i>Girroniera 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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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.