

# Evolutionary history of plant diversity on the Kunlun Mountains

Du Weibo<sup>1</sup>, Jia Peng<sup>1</sup>, Du Guozhen<sup>1</sup>

<sup>1</sup>State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou, Gansu Province, 730000, P. R. China

## Abstract

Large-scale patterns of biodiversity and the underlying mechanisms that regulate these patterns are central topics in biogeography and macroecology. The Qinghai-Tibetan Plateau (QTP) is a natural laboratory for studying these issues. However, most previous studies have focused on the entire QTP, and the independent physical geographical subunits in the region are not well understood. We studied the current plant diversity on the Kunlun Mountains, an independent physical geographical subunit located in northwest China, on the northern edge of the QTP. We integrated measures of species distribution, geological history, and phylogeography, and analyzed the taxonomic richness, origin time, and community phylogenetic structure of the plants present in the area. The distribution patterns of 1,911 seed plants highlighted that species were located mainly in the eastern regions of the Kunlun Mountains. Chinese endemic species of seed plants accounted for 29.8% of the total species on the Kunlun Mountains. The biodiversity patterns and mean divergence times (MDT) indicated that the eastern region of the Kunlun Mountains was the center for biodiversity conservation, particularly in the southeastern region, which has served as a museum for plant diversity on the Kunlun Mountains. According to the MDT, the origin time of the Kunlun Mountains' flora (KMF) was early Miocene (19.40 Ma), and the KMF is ancient. The biogeographical roles of the Kunlun Mountains were corridor and sink, and the corresponding key processes were species immigration and extinction. The extant biodiversity on the Kunlun Mountains has occurred through species recolonization after climatic fluctuations and glaciations during the Quaternary. The Kunlun Mountains also formed a barrier, representing a boundary among multiple floras, and converted the QTP into a closed physical geographical unit. The nearest taxon index indicated that habitat filtering may have played an important role in biodiversity patterns.

KEYWORDS: biodiversity, plant community, Kunlun Mountains, phylogeography, seed plants

## 1 | INTRODUCTION

Understanding biodiversity patterns at the regional scale has long been a major interest in macroecology and biogeography (Grierson et al., 2011; Ma, 2017; Patino et al., 2017). Numerous hypotheses have been proposed to explain these patterns. Some studies have suggested that contemporary environmental factors, such as climate and habitat heterogeneity, dominate the mechanisms currently mediating biodiversity (Kerr & Packer, 1997; Brown, Gillooly, Allen, Savage, & West, 2004; Currie et al., 2004; Wang, Brown, Tang, & Fang, 2009). Another hypothesis is that historical processes, such as speciation, extinction, and dispersal, predominantly influence biodiversity (Zobel, 1997; Ricklefs, 2005; Mittelbach et al., 2007). Notably, there is no universal theory that integrates the relative influences of contemporary environmental factors and historical processes on biodiversity patterns. However, numerous researchers consider that the

45 abiotic environment, contemporary biotic interactions, and evolutionary history simultaneously  
46 contribute to biodiversity patterns (Hawkins & Porter, 2003; Svenning & Skov, 2005, 2007;  
47 Montoya, Rodríguez, Zavala, & Hawkins, 2007; Wang, Fang, Tang, & Lin, 2012). Furthermore, it  
48 is difficult to distinguish the effects of collinearity between historical processes and contemporary  
49 environments.

50 Ecologists have proposed numerous hypotheses to explain species composition. The  
51 biodiversity patterns within a geographical region are the result of multiple processes, including  
52 speciation, extinction, migration, and ongoing species interactions (Lu et al., 2018). Moreover, the  
53 niche theory (Silvertown, 2004), neutral theory (Hubbell, 2005), and contemporary coexistence  
54 theory (Chu, Wang, Liu, Jiang, & He, 2017) have been used to reveal community assembly. The  
55 niche theory argues that species have different niches and that habitat filtering and competitive  
56 exclusion are the principal community assembly rules; this theory can be used to explore  
57 ecological and evolutionary processes at the regional scale (Mittelbach & Schemske, 2015;  
58 Baares-De-Dios et al., 2020). Regarding the neutral theory, it proposes that different species  
59 within an ecological community can have equivalent ecological functions, and models the process  
60 of community assembly as random (Hubbell, 2001). In recent years, ecologists have increasingly  
61 recognized that niche and neutral processes are not diametrically opposed and that both determine  
62 community assembly (Tilman, 2004; Chase, 2005; Gravel, Canham, Beaudet, & Messier, 2006;  
63 Leibold & McPeck, 2006). Regarding the contemporary coexistence theory, it assumes that inter-  
64 species differences are divided into two categories: niche differences and average fitness  
65 differences. The former are considered as stabilizing mechanisms that facilitate species  
66 coexistence, whereas the latter are regarded as equalizing mechanisms that promote competitive  
67 exclusion (Chu, Wang, Liu, Jiang, & He, 2017). Notably, the theory is yet to be assessed in  
68 communities at the regional scale.

69 Numerous studies have indicated that the abiotic environment, contemporary biotic interactions,  
70 and evolutionary history simultaneously contribute to the phylogenetic community structure at  
71 different scales (Webb, Ackerly, McPeck, & Donoghue, 2002; Kraft, Cornwell, Webb, & Ackerly,  
72 2007). Therefore, the phylogenetic community structure could help explain biodiversity patterns.  
73 In addition, the analysis of the community phylogenetic structure can facilitate the determination  
74 of the ecological and evolutionary processes that regulate biodiversity patterns at different scales.  
75 Evolutionary processes such as rapid *in situ* speciation, niche conservatism, and dispersal  
76 limitation can lead to phylogenetic clustering (Lu et al., 2018). In comparison, evolutionary  
77 processes such as niche evolution, convergent evolution, and colonization may lead to  
78 phylogenetic overdispersion within communities (Allen & Gillooly, 2006). Regarding ecological  
79 processes, habitat filtering and competitive exclusion can result in non-random community  
80 phylogenetic structures (Webb, Ackerly, McPeck, & Donoghue, 2002; Kraft, Cornwell, Webb, &  
81 Ackerly, 2007). Habitat filtering, which can lead to phylogenetic clustering, refers to the selection  
82 of certain species traits in a community (Wiens & Graham, 2005), whereas competitive exclusion  
83 might result in phylogenetic dispersion (Burns & Strauss, 2011).

84 Mountains are topographically complex regions that affect biodiversity and neighboring  
85 lowland ecosystem processes by facilitating biotic interchange, influencing regional climate, and  
86 nutrient runoff (Rahbek et al., 2019a). Notably, mountains reportedly disproportionately influence  
87 the global terrestrial biodiversity, particularly in the tropics, where they host hotspots with  
88 extraordinary levels of species richness. In the arctic and temperate regions, however, mountains

89 host few endemic species and typically have low species diversity, which barely exceed those of  
90 the adjacent lowlands (Rahbek et al., 2019b). Consequently, mountains offer natural laboratories  
91 for studying the mechanisms that govern biodiversity patterns at different scales.

92 The high mountains of China are mainly distributed on the Qinghai-Tibetan Plateau (QTP) and  
93 in adjacent regions (Wang, Wang, & Fang, 2004). The QTP refers to the plateau itself, which is the  
94 highest and most expansive plateau on the globe, occupying an area of 2.5 million km<sup>2</sup> with an  
95 average elevation of over 4,000 m (Zhang, Li, & Zheng, 2002). Extensive research has been  
96 conducted on the QTP, and the datasets thereby accumulated offer opportunities to investigate the  
97 biodiversity patterns and plant communities in such regions (Favre et al., 2015). Several studies  
98 have assessed the geographical distribution of species in the QTP (e.g., Wu, 2008; APGIV, 2016),  
99 but the complex environment of the QTP suggests that species richness would vary considerably  
100 across the region (Tang, Wang, Zheng, & Fang, 2006; Yang, Ma, & Krefl, 2013). Since the  
101 climatic fluctuations and glaciations of the Quaternary, the QTP has experienced four major  
102 glacial events (Shi, Li, & Li, 1998; Zhang, Li, & Zheng, 2002; Yi, Cui, & Xiong, 2005; Owen,  
103 Caffee, Finkel, & Seong, 2008; Owen & Dortch, 2014). These geological processes have driven  
104 radiation and species diversification in various groups of plants (Wen, Zhang, Nie, Zhong, & Sun,  
105 2014). However, these climatic fluctuations and glaciations have also led to mass extinction events  
106 in some areas of the QTP. According to the data from published monographs and literature, the  
107 QTP harbors ~10,000 species of vascular plants (Wu, 2008; APGIV, 2016), of which ~20% are  
108 endemic to the region (Wu, 2008; Yan, Yang, & Tang, 2013; Yu, Zhang, Liu, Chen, & Qi, 2018);  
109 the southern regions have especially high species richness (Mao et al., 2013).

110 Owing to major advancements in phylogeographic studies and tools, the evolutionary histories  
111 and underlying adaptations of plants in the QTP, including *Saussurea* (Wang, Susanna, Von Raab-  
112 Straube, Milne, & Liu, 2009), *Rheum* (Sun, Wang, Wan, Wang, & Liu, 2012), *Gentiana* (Favre et  
113 al., 2016), *Rhodiola* (Zhang, Meng, Allen, Wen, & Rao, 2014), *Saxifraga* (Ebersbach, Schnitzler,  
114 Favre, & Muellner-Riehl, 2017), and *Syncalathium* (Zhang, Nie, Wen, & Sun, 2011), among  
115 others (Qiu, Fu, & Comes, 2011; Liu, Luo, Li, & Gao, 2017), have become increasingly clear  
116 (Liu, Duan, Hao, Ge, & Sun, 2014). In addition, numerous researchers have integrated principles  
117 from different disciplines, including taxonomy, phylogeny, ecology, biogeography,  
118 phylogeography, and paleontology, to provide an insightful perspective to explore the  
119 regionalization of floristic assemblages (Li, Qian & Sun, 2018). Rapid speciation and habitat  
120 filtering have been reported to dominate the biodiversity and community assembly processes on  
121 the QTP, and the phylogenetic structure of vascular species is clustered in most regions of the QTP  
122 (Yan, Yang, & Tang, 2013). Recent studies have reported that the main phylogeographic patterns  
123 of seed plant species are contraction/recolonization, platform refugia/local expansion, and  
124 microrefugia in the Tibeto-Himalayan region (Muellner-Riehl, 2019). Numerous studies have also  
125 indicated that different floras each have their evolutionary history (e.g., Crisp & Cook, 2013;  
126 Baldwin, 2014; Linder & Verboom, 2015; Chen, Deng, Zhuo, & Sun, 2018; Lu et al., 2018). For  
127 example, the origin time of the Amazonian flora is 8.30 Ma (Hoorn, Wesselingh, Steege, &  
128 Bermudez, 2010), while the origin time of the Andes flora is 6.40 Ma (Särkinen, Pennington.,  
129 Lavin, Simon, & Hughes, 2012). Therefore, datasets from different regions provide the  
130 opportunity to explore the formation and maintenance mechanisms of biodiversity in these areas.  
131 That is, these datasets may contribute to our understanding of the plant diversity in the QTP.

132 Most previous studies have focused on the entire QTP, and there has been little research on the

133 independent physical geographical subunits in the region. The Kunlun Mountains are an  
134 independent physical geographical subunit with a relatively clear geographical range and plant  
135 distribution data; however, they are not classed as a biodiversity hotspot (Su, 1998; Zheng, 1999;  
136 Pan, 2000; Zachos & Habel, 2011; Wu, 2012–2015; Sun et al., 2015). In the present study, we  
137 used datasets from the region of the Kunlun Mountains to explore the evolutionary history of the  
138 plant diversity to: 1) estimate the origin time of the Kunlun Mountains' flora (KMF); 2) clarify  
139 when the extant plant diversity on the Kunlun Mountains emerged; and 3) reveal the phylogenetic  
140 structural patterns of seed plants in the region. An additional consequence among different regions  
141 of the Kunlun Mountains could help explore biodiversity conservation target.

142

## 143 **2 | MATERIALS AND METHODS**

### 144 **2.1 | Study area**

145 The Kunlun Mountains are an independent physical geographical subunit, located in northwest  
146 China, on the northern edge of the QTP. Geographically, they border the Pamirs Plateau to the  
147 west, southeast Qinghai to the east, the Qaidam and Tarim Basins to the north, and the northwest  
148 Tibet Autonomous Region to the south. The Kunlun Mountain range is oriented east–west and is  
149 located across 34°N–40°N and 75°E–100°E. The range extends for a total length of ~2,500 km  
150 and a width of 130–200 km. The mountain range is narrower in the west than in the east and  
151 covers a total area of over 500,000 km<sup>2</sup> (Wu, 2012–2015; Figure 1). The elevation of the mountain  
152 range increases from the east to the west, and ranges between 3,000 m and 7,719 m, with an  
153 average altitude of approximately 4,000 m.

154 The area has an annual precipitation that varies from ~100 to 500 mm and an average annual  
155 temperature below 0 °C. The annual precipitation is characterized by a decrease from the east to  
156 the west. The climate on the slopes of the mountain range varies greatly and the steep climate  
157 gradient results in a dramatic change in vegetation cover. From east to west, the vegetation types  
158 are alpine scrub, alpine meadow, and alpine steppe. In addition, there are a few coniferous forests  
159 in the east and west of the Kunlun Mountains (Zheng, 1999; Wu, 2012–2015).

160 To accurately reveal the current plant diversity, the study region was divided into 28 county-  
161 level geographical units according to the county area and vegetation type. Geographically, the  
162 Kunlun Mountains are divided into three regions: east, west, and center. The western region  
163 consists of six counties, the central region is composed of fourteen counties, with six counties on  
164 the southern slope and eight counties on the northern slope, and the eastern region comprises eight  
165 counties (Figure 2; Table 1).

166

### 167 **2.2 | Distribution data**

168 The basic distribution data were obtained from *Flora Kunlunica*, published in four volumes, by  
169 Wu and his colleagues (Wu, 2012–2015), with references to published monographs and other  
170 literature, including *Flora of Xinjiang* (Shen, 1993–2011), *Flora of Qinghai* (Liu, 1996–1999),  
171 *Flora of Tibet Autonomous Region* (Wu, 1983–1987), *The Vascular Plants and Their Eco-  
172 geographical Distribution of the Qinghai-Tibet Plateau* (Wu, 2008), and the National Specimen  
173 Information Infrastructure (<http://nsii.org.cn/2017/home.php>). Based on these data sources, and  
174 using the order of families from the Angiosperm Phylogeny Group IV (APGIV, 2016), the genera  
175 were classified into families according to *A Dictionary of the Families and Genera of Chinese  
176 Vascular Plants* (Li et al., 2018). All the species names were standardized following the Catalogue

177 of Life Checklist (<http://www.catalogueoflife.org/annual-checklist/2019/>) and The Plant List  
 178 (<http://www.theplantlist.org>). When species names differed between these two databases, these  
 179 names were standardized following The Plant List. Species that were not native to the Kunlun  
 180 Mountains were excluded, and infraspecific taxa were preserved. Overall, the information that was  
 181 collected presented a comprehensive checklist of the seed plant species on the Kunlun Mountains.  
 182 To analyze spatial patterns, each species was assigned to a county-level geographical unit based on  
 183 species distribution data.

184

### 185 **2.3 | Origin and divergence time of floras**

186 To obtain datasets pertinent to the ages of the KMF, we collected data from published molecular  
 187 phylogenetic and biogeographical studies, following two principles of data collection: genera from  
 188 the KMF had to be included and the ages and the ancestral areas of these genera had to be  
 189 available. On the basis of the corresponding data, mean divergence times (MDT) were calculated  
 190 as:

$$191 \quad MDT = \frac{(AGE_1 \times S_1) + (AGE_2 \times S_2) + (AGE_3 \times S_3) + \dots + (AGE_n \times S_n)}{S_1 + S_2 + S_3 + \dots + S_n}$$

192 where  $AGE_i$  is the age of the genus  $i$  ( $i = 1, \dots, n$ ) in a sample, and  $S_i$  is the species number of  
 193 the genus  $i$  in the sample.

194 The standardized effect size of the mean divergence time (SES-MDT) of the genera in the  
 195 sample was calculated as:

$$196 \quad SES - MDT = \frac{MDT_{observed} - MDT_{random}}{s.d. (MDT_{random})}$$

197 where  $MDT_{observed}$  represents observed MDT,  $MDT_{random}$  represents the expected MDT of the  
 198 randomized assemblages ( $n=999$ ), and  $s.d. (MDT_{random})$  is the standard deviation of the MDT for  
 199 the randomized assemblages. For the youngest quartile, samples with values of SES-MDT below -  
 200 1.96 were confirmed as significantly young floras, whereas, for the oldest quartile, samples with  
 201 SES-MDT values above 1.96 were confirmed as significantly ancient floras (Lu et al., 2018).

202 To accurately reveal the evolutionary history of KMF, we calculated the origin and divergence  
 203 time of plants in county-level geographical units and different regions.

204

### 205 **2.4 | Phylogenetic structure**

206 We calculated the nearest taxon index (NTI), at the species level, in each county. The  
 207 corresponding NTI were calculated to analyze the community phylogenetic structure (i.e.,  
 208 clustering or overdispersion), and to examine possible ecological and evolutionary processes  
 209 within communities (Webb, Ackerly, McPeck, & Donoghue, 2002). Each NTI was based on the  
 210 mean nearest taxon distance (MNTD), which is an estimate of the mean phylogenetic relatedness  
 211 between each pair of taxa in a sample and its nearest relative in a phylogeny. The NTI reflects the  
 212 structure in the shallower parts of a phylogeny (Webb, Ackerly, McPeck, & Donoghue, 2002). At  
 213 the community level, positive NTI values indicate phylogenetic clustering, whereas negative  
 214 values indicate phylogenetic dispersion. The NTI values were calculated as follows:

215 
$$NTI = -1 \times \frac{MNTD_{observed} - MNTD_{random}}{s.d.(MNTD_{random})}$$

216 where  $MNTD_{observed}$  represents the observed MNTD values,  $MNTD_{random}$  represents the mean  
 217 values of the expected MNTD in the randomized assemblages ( $n = 999$ ), and  $s.d.(MNTD_{random})$  is  
 218 the standard deviations of the  $MNTD_{random}$  values in the randomized assemblages. The null  
 219 distributions of MNTD were created by randomly selecting the observed number of taxa in each  
 220 sample 999 times, with all the taxa in the phylogeny serving as the sampling pool.

221 Phylogenetic analyses require a phylogenetic tree of seed plants, the phylogenetic tree was  
 222 constructed using Phylomatic (<http://phylodiversity.net/phyloomatic/>) with the stored tree data from  
 223 Zanne et al. (2014). Ecological index was calculated using R version 3.3.3 (R Core Team, 2017)  
 224 and picante packages (Kembel et al., 2010).

225

## 226 **3 | RESULTS**

### 227 **3.1 | Taxa richness**

228 A total of 1,911 seed plants, including subspecies and varieties, have been recorded on the  
 229 Kunlun Mountains, and they belonged to 397 genera, 75 families, and 32 orders. Gymnosperms  
 230 accounted for only 26 of these seed plant species, which were further classified into 5 genera, 3  
 231 families, and 3 orders (Figure 3c). The remaining seed plants were all angiosperms.

232 The seed plants of the KMF comprised 226 woody species and 1,685 herbaceous species  
 233 (Figure 3a). Specifically, the woody species consisted in 22 tree species, 197 shrub species, and 7  
 234 liana species. The herbaceous species were represented by 9 herbaceous climber species, 224  
 235 annual herb species, and 1,452 perennial herb species. There were 570 species endemic to China,  
 236 corresponding to 29.83% of the total and including 81 woody species and 489 herbaceous species.  
 237 The KMF seed plants were divided into 39 woody genera, 347 herbaceous genera, and 11 genera  
 238 that include both woody and herbaceous species (Figure 3b). Overall, 7 of these genera (all  
 239 herbaceous genera) were endemic to China, and six were only distributed in the eastern region of  
 240 the Kunlun Mountains. Approximately a third of the plant species were distributed across 15  
 241 genera, with more than 20 species in each genus. Conversely, there were 155 genera that contained  
 242 only one species each. At the genus level, there were 336, 248, and 245 seed plant genera in the  
 243 eastern, central, and western regions of the Kunlun Mountains, respectively. In addition, 198 and  
 244 192 genera were encountered on the northern and southern slopes of the Middle Kunlun  
 245 Mountains, respectively.

246 Overall, the KMF biodiversity varied spatially (Table 1), with the eastern region of the Kunlun  
 247 Mountains showing higher biodiversity than the western and central regions (Table 1). Similar  
 248 results also characterized the genera richness on the Kunlun Mountains, and genera richness was  
 249 higher in the southeastern regions. The distribution patterns of seed plants indicated that species  
 250 and genera were distributed mainly in the eastern region, especially the southeastern region (Table  
 251 1; Supplementary Tables).

252

### 253 **3.2 | Origin and divergence time of floras**

254 In this study, 126 clades of seed plants (species or genus level) were collected, accounting for  
 255 126 genera, 55 families, and 30 orders of seed plants. Notably, there were 5 clades of  
 256 gymnosperms and 121 clades of angiosperms. The 5 clades represent all gymnosperm species,

257 while the 121 clades of angiosperms represent 61% of the species, 31% of the genera, 72% of the  
258 families, and 93% of the orders in angiosperms, and the mean divergence time of these clades  
259 could thus represent the origin time of the KMF.

260 The origin time of the KMF is early Miocene (19.40 Ma). The MDT in the eastern, central, and  
261 western regions of the Kunlun Mountains was of 20.07 Ma, 17.55 Ma, and 18.09 Ma,  
262 respectively. In addition, the MDT was 17.60 Ma and 17.18 Ma on the northern and southern  
263 slopes of the Middle Kunlun Mountains, respectively. Across the different county-level  
264 geographical units, the maximum MDT was 22.77 Ma, in Banma, and the minimum MDT was  
265 17.28 Ma, in Minfeng. Four of the SES-MDT, namely in Banma, Maqin, Qumalai, and Wuqia,  
266 showed significant differences ( $P < 0.05$ ; Table 2). These significant SES-MDT revealed that the  
267 flora lineages were more ancient in Banma and Maqin ( $P < 0.05$ ) and more recent in Qumalai and  
268 Wuqia ( $P < 0.05$ ; Table 2). Overall, MDT values were greater in both ends of the areas, and the  
269 eastern flora was older than the western flora (Table 2). However, the origin times of the 24  
270 counties did not show significant differences.

271

### 272 3.3 | Phylogenetic structure

273 The NTI indicated that the counties had different phylogenetic structures (Figure 4). The  
274 respective NTI values of 27 county-level communities were positive, and the 22 of these NTI  
275 values were statistically significant ( $P < 0.05$ ). Furthermore, only the Banma community was  
276 negative NTI and showed significant differences ( $P < 0.05$ ; Figure 4). Five additional counties,  
277 namely Jiuzhi, Minfeng, Yutian, Zhiduo, and Bange, had negative NTI values but these were not  
278 statistically significant. Notably, Jiuzhi is located in the southeastern region, while the other  
279 counties belong to the central regions and Minfeng and Yutian are adjacent to the Tarim Basins  
280 (Figure 2).

281

## 282 4 | DISCUSSION

### 283 4.1 | Biodiversity patterns on the Kunlun Mountains

284 These gymnosperms were Pinaceae, Ephedraceae, and Cupressaceae. The Pinaceae consisted of  
285 3 genera, while the Ephedraceae and Cupressaceae were represented by 1 genus each. Notably, 2  
286 genera that belonged to the Pinaceae, namely *Abies* and *Larix*, were only distributed in Banma,  
287 which is located in the southeastern region of the Kunlun Mountains. At the species level, there  
288 were 18, 8, and 9 gymnosperm species in the eastern, central, and western regions of the Kunlun  
289 Mountains, respectively. In addition, there were 7 and 4 gymnosperm species on the northern and  
290 southern slopes of the Middle Kunlun Mountains, respectively. At the genus level, gymnosperms  
291 were present in the eastern region of the Kunlun Mountains with 3 families, accounting for 5  
292 genera, while there were 3 genera, belonging to 3 families, in the central and western regions.  
293 Moreover, there were 3 and 2 gymnosperm genera on the north and south slopes of the Middle  
294 Kunlun Mountains, respectively. Therefore, the eastern region is higher biodiversity in the Kunlun  
295 Mountains, particularly in the southeastern region. Similar results also characterized the  
296 angiosperms on the Kunlun Mountains.

297 Some studies have suggested that the diversity hotspots of Chinese endemic seed flora are on  
298 the Qinling Mountains and further south, or on the Hengduan Mountains and in eastern China  
299 (Huang et al., 2016). Similar patterns have been identified for the hotspots of endemic woody seed  
300 plants in China (Huang et al., 2012). That is, the Kunlun Mountains have not been identified as a

301 hotspot for Chinese endemic seed flora or a center of diversification for extant plants.  
302 Approximately 20% of the total species are endemic to the QTP (Wu, 2008; Yan, Yang, & Tang,  
303 2013; Yu, Zhang, Liu, Chen, & Qi, 2018), and 32.4% of the total species are endemic to the  
304 Hengduan Mountains (Zhang, Boufford, Ree, & Sun, 2009). Consequently, the Chinese endemic  
305 species found on the Kunlun Mountains that were reported in the present study may have  
306 dispersed from other areas that served as speciation centers. The species richness and genera  
307 richness of the KMF highlighted that the eastern region of the Kunlun Mountains represents a  
308 center for biodiversity conservation, particularly in the southeastern region, which we consider as  
309 an important conservation target.

310

#### 311 **4.2 | Evolutionary history of plant diversity on the Kunlun Mountains**

312 Our results indicated that the KMF is ancient (i.e., origin time: of 19.40 Ma) compared with  
313 other floras of the Northern Hemisphere (Baldwin, 2014; Chen, Deng, Zhuo, & Sun, 2018). For  
314 instance, the origin time of the Californian flora was 10.60 Ma (Baldwin, 2014). Moreover, the  
315 KMF is older than the Australian flora (18.80 Ma; Crisp & Cook, 2013), the South African flora  
316 (18.70 Ma; Linder & Verboom, 2015), the flora of western China (15.29–18.86 Ma; Lu et al.,  
317 2018), and East Asian flora (15.10 Ma; Chen, Deng, Zhuo, & Sun, 2018). In addition, the origin  
318 time of the KMF in the eastern region was greater than that in the central and western regions;  
319 therefore, the eastern region of KMF is the most ancient.

320 In county-level geographical units, the origin time of floras was divided into four categories:  
321 MDT > 22 Ma, 22 Ma > MDT > 20 Ma, 20 Ma > MDT > 18 Ma, and MDT < 18 Ma. Only one  
322 county-level flora was older than 22 Ma, namely Banma, and the SES-MDT of Banma was 4.21.  
323 Therefore, the Banma flora was the most ancient (22.53 Ma), and should thus be an important  
324 conservation target. Furthermore, there were 4 county-level floras that originated between 20 Ma  
325 and 22 Ma, namely Jiuzhi, Maqin, Zhiduo, and Yecheng, while 21 county-level floras had an  
326 origin time between 18 Ma and 20 Ma. Finally, the floras of Qiemo and Minfeng were less than 18  
327 Ma, and they were located on the northern slope of the Middle Kunlun Mountains. The Minfeng  
328 flora was the youngest, with an origin time of 17.28 Ma. In addition, four SES-MDT, namely the  
329 Banma, Maqin, Qumalai, and Wuqia floras, showed significant differences ( $P < 0.05$ ). The origin  
330 time of the floras in Qumalai and in Wuqia was 18.34 Ma and 18.11 Ma, respectively. These floras  
331 had more recent lineages ( $P < 0.05$ ) and thus were young.

332 The geological history and uplifts of the QTP are still being debated because the QTP consists  
333 of multiple physical geographical subunits, which have experienced different geological histories  
334 and uplifts (Sun and Zheng, 1998; Spicer et al., 2003; Renner, 2016; Deng et al., 2017; Spicer et  
335 al., 2020). Spicer et al. (2020) reported that the formation of the QTP only occurred in the late  
336 Neogene. Moreover, recent studies have indicated that the formation of the Asian monsoon system  
337 also began in the Neogene (Li et al., 2021; Xie et al., 2021). Other studies have recently  
338 demonstrated that the current QTP ecosystem began in the early Miocene (Deng, Wu, Wang, Su,  
339 & Zhou, 2019), and that the Kunlun Mountains have reached their present height over the last 17  
340 million years (Pan, 2000; Sun et al., 2015). In addition, the arid climate of Central Asia appeared  
341 in the late Miocene, with an origin time of 5.3 Ma (i.e., 5.23–5.38 Ma), and multiple climate  
342 fluctuations have occurred since the early Pliocene, especially the Quaternary (Zhang & Sun,  
343 2011; Zhang, Li, Wang, & Zhang, 2021). After the early Pliocene, the Kunlun Mountains  
344 experienced the Kunhuang movement (1.1 Ma; Cui et al., 1998) and numerous glacial events (Su,

345 1998). Hence, the extant biodiversity patterns of the KMF might begin in the early Pliocene (5.3  
346 Ma).

347 Since the Quaternary, the Kunlun Mountains have also experienced dramatic climatic  
348 fluctuations (Deng, Wu, Wang, Su, & Zhou, 2019) and numerous glacial events (Su, 1998; Owen,  
349 Caffee, Finkel, & Seong, 2008; Owen & Dortch, 2014; Renner, 2016), including the Largest  
350 Glaciation (1.2–0.6 Ma) and the Last Glacial Maximum (Shi, Zheng, & Yao, 1997; Liu, Duan,  
351 Hao, Ge, & Sun, 2014). These numerous glaciations have led to mass extinction events on the  
352 Kunlun Mountains. A recent study has highlighted that the main phylogeographical patterns of  
353 seed plant species in the Tibeto-Himalayan region are contraction/recolonization, platform refugia/  
354 local expansion, and microrefugia (Muellner-Riehl, 2019). However, studies have also indicated  
355 that there are no Chinese endemic species in the platform refugia and microrefugia, and few  
356 species are present in these refugia (López-Pujol, Zhang, Sun, Ying, & Ge, 2011; Muellner-Riehl,  
357 2019). In addition, another study has suggested that there are no platform refugia on the Kunlun  
358 Mountains (Yu et al., 2018). Consequently, after the abovementioned glacial events, the  
359 biodiversity patterns might have dispersed from refugia adjacent to the Kunlun Mountains.  
360 Notably, we speculate that the extant biodiversity patterns were primarily formed during the  
361 Quaternary (2.6 Ma).

362 Overall, the origin time of the KMF (19.40 Ma) was found to be much greater than 5.3 Ma. In  
363 addition, the Kunlun Mountains were not identified as a hotspot of Chinese endemic seed flora nor  
364 a center of diversification for extant plants (Huang et al., 2012; Huang et al., 2016). According to  
365 the phylogeographical regions of the Chinese flora, the Kunlun Mountains are in the transition  
366 zone between the Tethyan region and the QTP (Ye et al., 2019; Ye, Liu, & Chen, 2020). Therefore,  
367 the extant biodiversity on the Kunlun Mountains has likely occurred through species  
368 recolonization after the climatic fluctuations and glaciations of the Quaternary. The  
369 biogeographical roles of the Kunlun Mountains were corridor and sink, and the corresponding key  
370 processes were species immigration and extinction. In addition, the Kunlun Mountains also  
371 represented a barrier and a boundary among the Tethyan region, the QTP, and East Asia.

372

### 373 **4.3 | Patterns of phylogenetic structure on the Kunlun Mountains**

374 The evolutionary history of taxa has an impact, particularly on the net relatedness index (Webb,  
375 Ackerly, McPeck, & Donoghue, 2002). The extant biodiversity on the Kunlun Mountains occurred  
376 by species recolonization, and complex species recolonization was likely the most important  
377 evolutionary process affecting the deeper phylogenetic community structure. NTI analyses can  
378 help reveal the phylogenetic structure in a community, and the NTI primarily reflect the structure  
379 in the shallower parts of a phylogeny. The complex sources of species colonization had little effect  
380 on NTIs. Therefore, only the NTI was calculated. When the NTI values were not significantly  
381 different, the community assembly tended to be random. Similarly, when the NTI was closer to 0,  
382 the community assembly tended to be more random. Conversely, the niche theory may reveal the  
383 community assembly.

384 Ecologists have indicated that the abiotic environment, contemporary biotic interactions, and  
385 evolutionary history simultaneously contribute to the community phylogenetic structure at  
386 different scales (Webb, Ackerly, McPeck, & Donoghue, 2002; Kraft, Cornwell, Webb, & Ackerly,  
387 2007). Previous studies have revealed that abiotic determinism tends to increase with spatial scale,  
388 while biotic determinism tends to decrease with spatial scale. Notably, abiotic determinism is

389 more important than biotic interactions in biodiversity maintenance mechanisms at the regional  
390 scale (Charles et al., 2010; Cardillo, 2011; Niu, Wang, Lian, Ye, & Shen, 2011; Villalobos, Rangel,  
391 & Diniz-Filho, 2013; Yang et al., 2014). Therefore, the abiotic environment and evolutionary  
392 history of biodiversity patterns greatly influence the community phylogenetic structure in county-  
393 level geographical units.

394 On the Kunlun Mountains, only one NTI, namely Banma, indicated that the community  
395 phylogenetic structure was dispersed. The other NTI values revealed that the community  
396 phylogenetic structures were clustered in the other counties. In the western region of the Kunlun  
397 Mountains, the community phylogenetic structure was clustered, as highlighted by the NTI values.  
398 Similarly, in the central region of the Kunlun Mountains, all the NTI values revealed clustered  
399 community phylogenetic structures. Notably, the four positive NTI values, namely Minfeng,  
400 Yutian, Zhiduo, and Bange, were greater than 1.5, although they were not significantly different.  
401 Finally, in the eastern region of the Kunlun Mountains, seven NTI values were positive, six of the  
402 NTIs showed significant differences ( $P < 0.05$ ). Only one positive NTI was 0.46, and did not show  
403 significant, namely Jiuzhi. Only one NTI was negative, and showed significant differences ( $P <$   
404  $0.05$ ).

405 The positive NTI values indicated that habitat filtering determined the corresponding  
406 community assemblies. Based on the vegetation type, forests were concentrated in Banma,  
407 whereas Jiuzhi was dominated by alpine scrubs. The MDT of the floras in Banma and Jiuzhi were  
408 greater than 20 Ma, which highlights these are ancient floras, and these two counties have served  
409 as museums for plant diversity on the Kunlun Mountains. Notably, the combination of species  
410 from multiple floras and adequate hydrothermal conditions may explain the community  
411 phylogenetic structures in Banma and Jiuzhi.

412

## 413 **5 | CONCLUSIONS**

414 The biodiversity patterns and MDT values indicated that the eastern region of the Kunlun  
415 Mountains is a center for biodiversity conservation, particularly in the southeastern region, which  
416 has served as a museum for plant diversity on the Kunlun Mountains. However, compared with  
417 the flora in the southeastern part of the QTP, the KMF has a relatively low conservation value on  
418 the QTP, which is consistent with the findings of previous studies (Mao et al., 2013; Yan, Yang, &  
419 Tang, 2013; Lu et al., 2018).

420 The origin time of the KMF was early Miocene (19.40 Ma). The KMF was ancient, although  
421 the extant biodiversity on the Kunlun Mountains has occurred through species recolonization after  
422 the climatic fluctuations and glaciations of the Quaternary. The biogeographical roles of the  
423 Kunlun Mountains were those of corridor and sink, and the related key processes were species  
424 immigration and extinction. In addition, the Kunlun Mountains also functioned as a barrier,  
425 representing a boundary among the Tethyan region, the QTP, and East Asia. The Kunlun  
426 Mountains have converted the QTP into a closed physical geographical unit.

427 In the QTP, the responses of species diversity to climate obviously depend on the biotype. The  
428 diversity of woody plants was more strongly associated with climate than that of herbaceous  
429 plants. Energy and water availability jointly rule the diversity of woody plants, whereas water  
430 availability predominantly regulates the diversity of herbaceous plants (Yan, Yang, & Tang, 2013).  
431 On the Kunlun Mountains, the dominant vegetation type consists of herbaceous plants, although  
432 there are a few coniferous forests in the eastern and western regions of the Kunlun Mountains.

433 Furthermore, the annual precipitation notably decreases from the east to the west (Zheng, 1999;  
434 Wu, 2012–2015), while there are abundant rivers in the west and east (Figure 2). Notably, the NTI  
435 values indicated that habitat filtering determined these community assemblies. Therefore, we  
436 conclude that species recolonization and habitat filtering may have contributed to the present plant  
437 diversity of the Kunlun Mountains via ecological and evolutionary processes, and habitat filtering  
438 may play an important role in ecological processes, particularly in terms of water availability.  
439

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446

#### 447 **Competing Interests**

448 The authors have no conflict of interest to declare.  
449

#### 450 **Data Accessibility**

451 Data are available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1rn8pk0t2>  
452

#### 453 **Author Contributions**

454 Du Weibo collected basic data, organized data, posed scientific questions, and wrote the  
455 manuscript; Jia Peng calculated the mean divergence times, standardized the effect sizes of the  
456 mean divergence times, and the nearest taxon index in each county; Du Guozhen guided this  
457 study.  
458

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745 **TABLE 1** The plant diversity of 28 counties on the Kunlun Mountains.

<b>East Kunlun Mountains (EK)</b>				<b>North slope of Middle Kunlun Mountains (NMK)</b>			
Counties	Families	genera	Species	Counties	Families	genera	Species
Banma (BM)	58	182	391	Dulan (DL)	37	108	243
Jiuzhi (JZ)	53	193	536	Geermu (GRM)	37	122	281
Dari (DR)	43	119	288	Ruoqiang (RQ)	37	124	294
Gande (GD)	32	73	153	Qiemu (QM)	31	81	157
Chenduo (CD)	47	179	490	Minfeng (MF)	24	51	69
Maduo (MD)	43	140	471	Yutian (YT)	32	72	120
Maqin (MQ)	60	234	749	Cele (CL)	36	109	198
Xinghai (XH)	58	236	731	Hetian (HT)	37	93	177
Total	73	337	1299	Total	53	198	639
<b>South slope of Middle Kunlun Mountains (SMK)</b>				<b>West Kunlun Mountains (WK)</b>			
Counties	Families	genera	Species	Counties	Families	genera	Species
Qumalai (QML)	41	143	360	Pishan (PS)	36	98	173
Zhiduo (ZD)	31	76	162	Yecheng (YC)	48	160	388
Bange (BG)	34	70	129	Shache (SC)	34	79	115
Nima (NM)	23	50	109	Taxian (TX)	50	177	492
Gaize (GZ)	27	68	114	Aketao (AKT)	49	151	340
Ritu (RT)	37	127	263	Wuqia (WQ)	42	160	318
Total	45	192	602	Total	59	245	813

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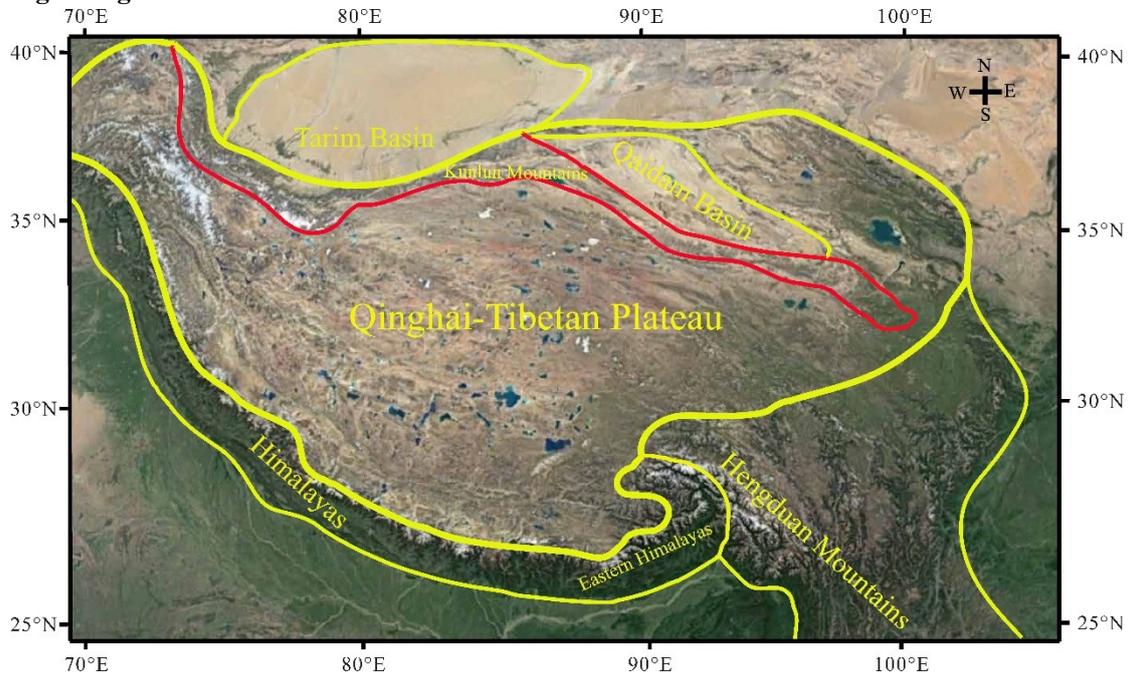
747 **TABLE 2** The mean divergence times (MDTs) of 28 counties on the Kunlun Mountains.

<b>East Kunlun Mountains (EK)</b>				<b>North slope of Middle Kunlun Mountains (NMK)</b>			
Counties	MDTs (Ma)	SES-MDTs	P-value	Counties	MDTs (Ma)	SES-MDTs	P-value
Banma (BM)	22.53	4.21	0.002	Dulan (DL)	18.21	-1.67	0.049
Jiuzhi (JZ)	20.61	1.67	0.042	Geermu (GRM)	18.57	-1.36	0.084
Dari (DR)	19.61	-0.06	0.465	Ruoqiang (RQ)	18.79	-1.13	0.134
Gande (GD)	18.81	0.16	0.422	Qiemu (QM)	17.74	-1.69	0.044
Chenduo (CD)	19.74	0.20	0.414	Minfeng (MF)	17.28	-1.37	0.087
Maduo (MD)	19.44	-0.42	0.356	Yutian (YT)	18.88	-1.46	0.065
Maqin (MQ)	20.97	2.87	0.004	Cele (CL)	18.25	-1.29	0.096
Xinghai (XH)	18.87	0.46	0.322	Hetian (HT)	19.39	-0.28	0.401
<b>South slope of Middle Kunlun Mountains (SMK)</b>				<b>West Kunlun Mountains (WK)</b>			
Counties	MDTs (Ma)	SES-MDTs	P-value	Counties	MDTs (Ma)	SES-MDTs	P-value
Qumalai (QML)	18.34	-1.99	0.023	Pishan (PS)	18.84	-0.81	0.222
Zhiduo (ZD)	20.75	1.13	0.135	Yecheng (YC)	20.13	0.72	0.245
Bange (BG)	19.29	-0.34	0.356	Shache (SC)	19.94	0.21	0.401
Nima (NM)	18.50	-1.08	0.148	Taxian (TX)	18.79	-1.44	0.076

Gaize (GZ)	18.98	-0.51	0.295	Aketao (AKT)	19.49	-0.21	0.430
Ritu (RT)	19.20	-0.56	0.288	Wuqia (WQ)	18.11	-1.76	0.033

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749 **Figure legends**



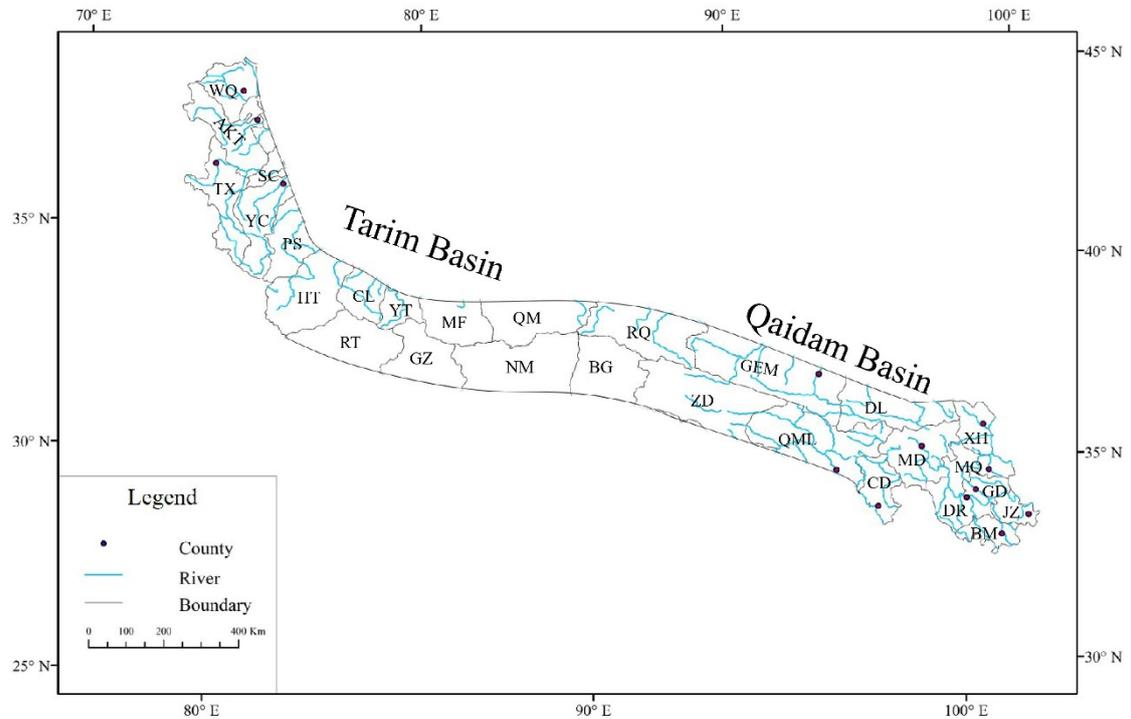
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752 **FIGURE 1** Geographical location of the Kunlun Mountains, China (outlined in red).

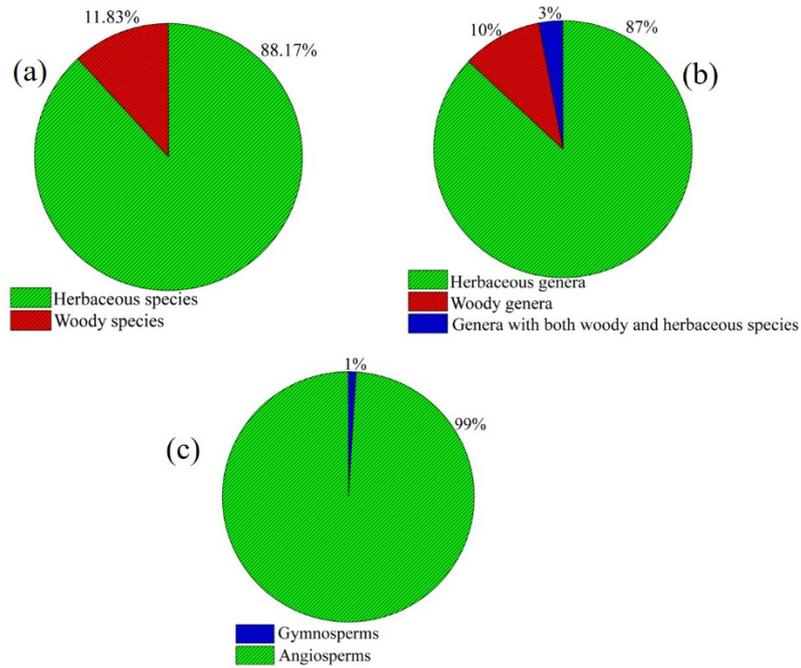
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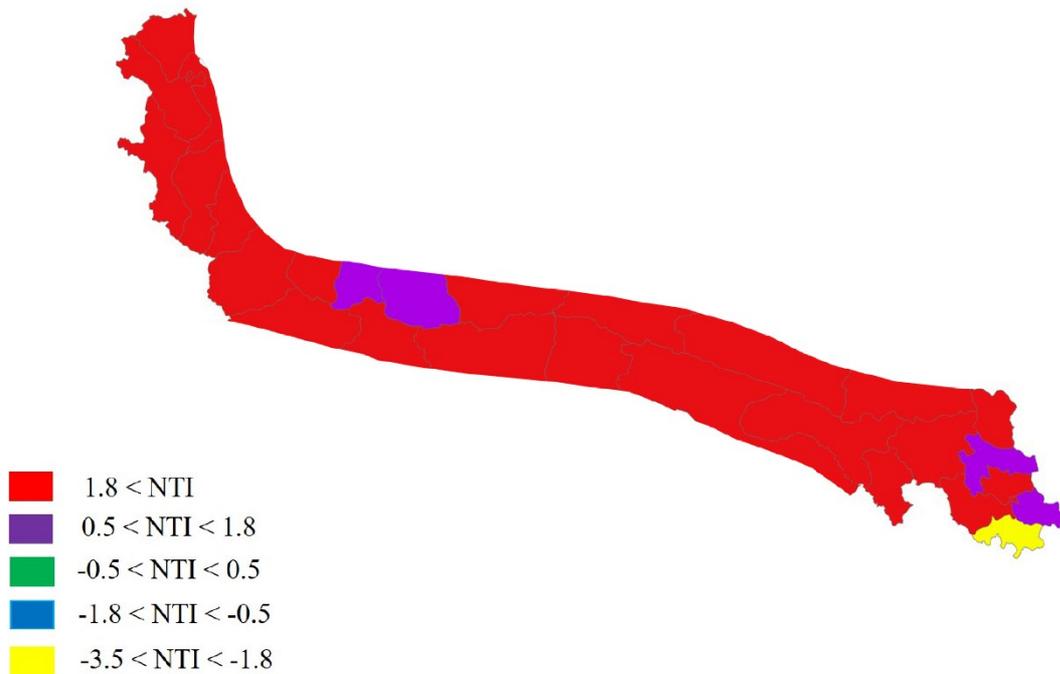


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756 **FIGURE 2** The county-level geographical units of the Kunlun Mountains, China.  
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 759 **FIGURE 3** Taxonomic richness in the Kunlun Mountains. (a) Species richness of woody and  
 760 herbaceous plants, (b) genera richness of woody and herbaceous plants, and (c) gymnosperms and  
 761 angiosperms of seed plants.  
 762



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 765 **FIGURE 4** Patterns of nearest taxon index (NTI) at the county-level geographical units of the  
 766 Kunlun Mountains.

