

Evolutionary history of plant diversity on the Kunlun Mountains

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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

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

The high mountains of China are mainly distributed on the Qinghai-Tibetan Plateau (QTP) and in adjacent regions (Wang, Wang, & Fang, 2004). The QTP refers to the plateau itself, which is the highest and most expansive plateau on the globe, occupying an area of 2.5 million km² with an average elevation of over 4,000 m (Zhang, Li, & Zheng, 2002). Extensive research has been conducted on the QTP, and the datasets thereby accumulated offer opportunities to investigate the biodiversity patterns and plant communities in such regions (Favre et al., 2015). Several studies have assessed the geographical distribution of species in the QTP (e.g., Wu, 2008; APGIV, 2016), but the complex environment of the QTP suggests that species richness would vary considerably across the region (Tang, Wang, Zheng, & Fang, 2006; Yang, Ma, & Kreft, 2013). Since the climatic fluctuations and glaciations of the Quaternary, the QTP has experienced four major glacial events (Shi, Li, & Li, 1998; Zhang, Li, & Zheng, 2002; Yi, Cui, & Xiong, 2005; Owen, Caffee, Finkel, & Seong, 2008; Owen & Dortch, 2014). These geological processes have driven radiation and species diversification in various groups of plants (Wen, Zhang, Nie, Zhong, & Sun, 2014). However, these climatic fluctuations and glaciations have also led to mass extinction events in some areas of the QTP. According to the data from published monographs and literature, the QTP harbors ~10,000 species of vascular plants (Wu, 2008; APGIV, 2016), of which ~20% are endemic to the region (Wu, 2008; Yan, Yang, & Tang, 2013; Yu, Zhang, Liu, Chen, & Qi, 2018); the southern regions have especially high species richness (Mao et al., 2013).

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

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

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

2 | MATERIALS AND METHODS

2.1 | Study area

The Kunlun Mountains are an independent physical geographical subunit, located in northwest China, on the northern edge of the QTP. Geographically, they border the Pamirs Plateau to the west, southeast Qinghai to the east, the Qaidam and Tarim Basins to the north, and the northwest Tibet Autonomous Region to the south. The Kunlun Mountain range is oriented east–west and is located across 34°N–40°N and 75°E–100°E. The range extends for a total length of ~2,500 km and a width of 130–200 km. The mountain range is narrower in the west than in the east and covers a total area of over 500,000 km² (Wu, 2012–2015; Figure 1). The elevation of the mountain range increases from the east to the west, and ranges between 3,000 m and 7,719 m, with an average altitude of approximately 4,000 m.

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

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

2.2 | Distribution data

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

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

2.3 | Origin and divergence time of floras

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

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

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 the genus i in the sample.

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

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

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

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

2.4 | Phylogenetic structure

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

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

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

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

3 | RESULTS

3.1 | Taxa richness

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

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

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

3.2 | Origin and divergence time of floras

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

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

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

3.3 | Phylogenetic structure

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

4 | DISCUSSION

4.1 | Biodiversity patterns on the Kunlun Mountains

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

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

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

4.2 | Evolutionary history of plant diversity on the Kunlun Mountains

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

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

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

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

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

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

4.3 | Patterns of phylogenetic structure on the Kunlun Mountains

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

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

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

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

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

5 | CONCLUSIONS

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

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

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

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

Acknowledgments

We thank the previous generations of Chinese botanists who have conducted extensive research on the plants of the region evaluated in this study.

This study was supported by the Key Program of the National Natural Science Foundation of China (No. 41671038) and the National Key Research and Development Program of China (2017YFC0504801).

Competing Interests

The authors have no conflict of interest to declare.

Data Accessibility

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

Author Contributions

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

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744

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

East Kunlun Mountains (EK)				North slope of Middle Kunlun Mountains (NMK)			
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
South slope of Middle Kunlun Mountains (SMK)				West Kunlun Mountains (WK)			
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

746

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

East Kunlun Mountains (EK)				North slope of Middle Kunlun Mountains (NMK)			
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
South slope of Middle Kunlun Mountains (SMK)				West Kunlun Mountains (WK)			
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

Figure legends

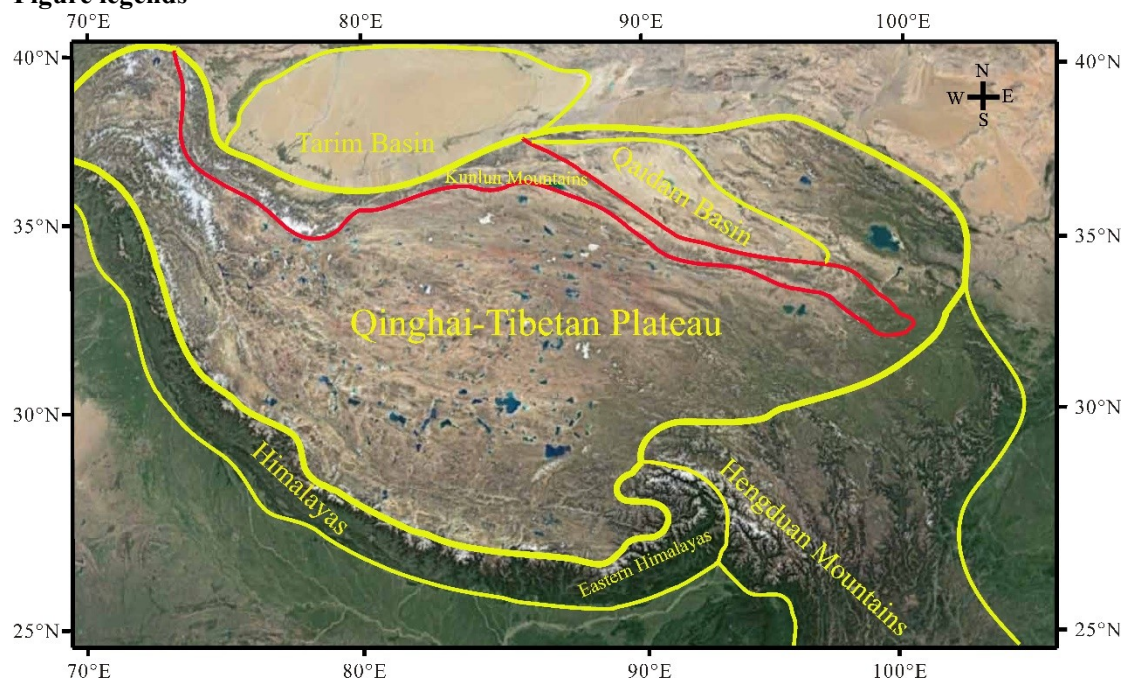


FIGURE 1 Geographical location of the Kunlun Mountains, China (outlined in red).

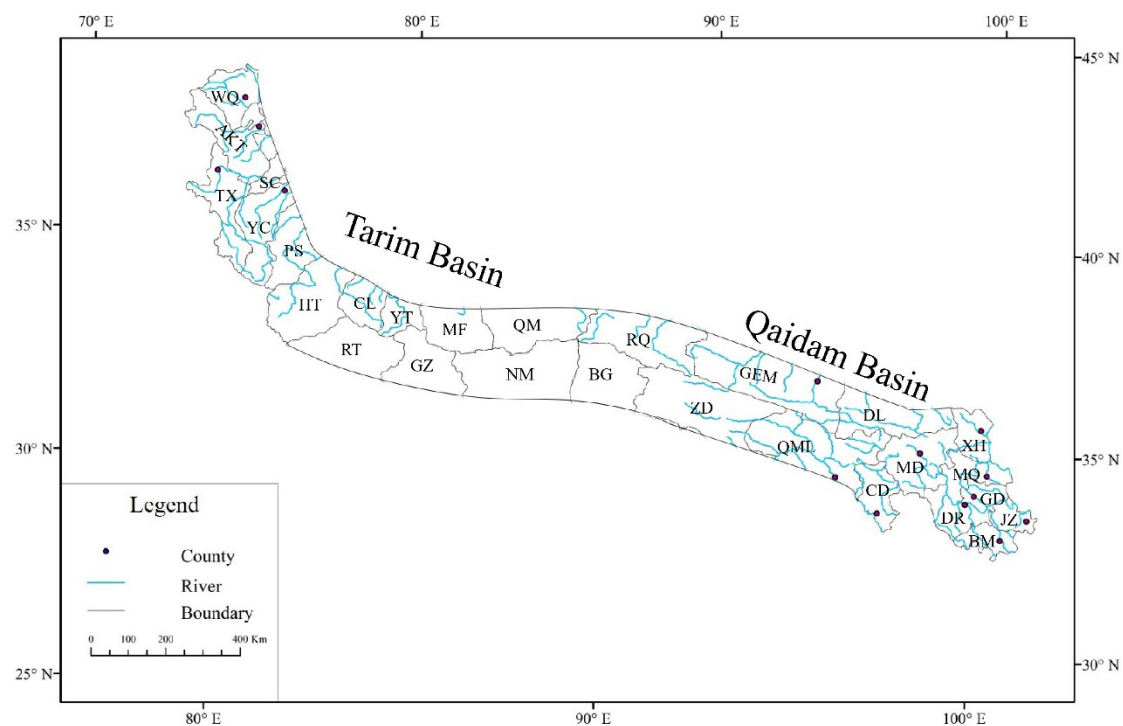


FIGURE 2 The county-level geographical units of the Kunlun Mountains, China.

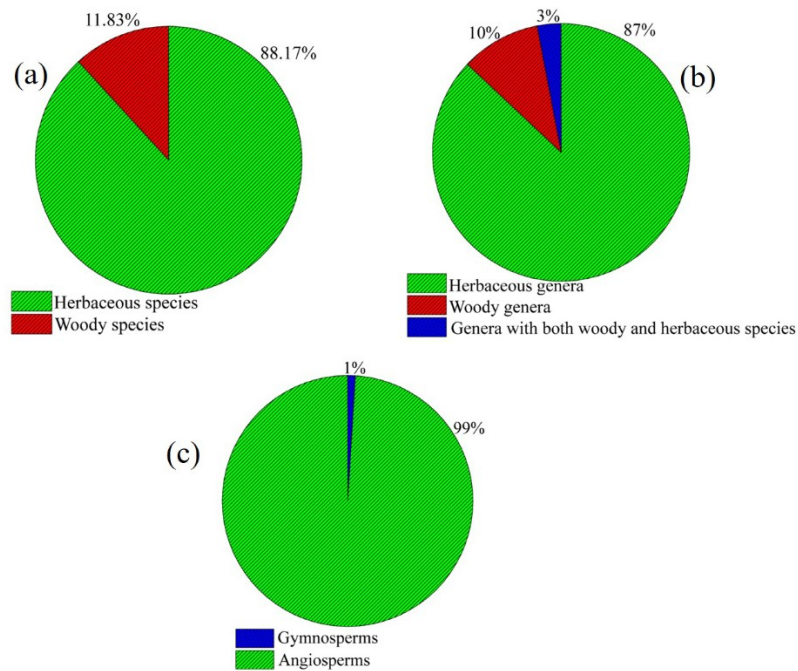


FIGURE 3 Taxonomic richness in the Kunlun Mountains. (a) Species richness of woody and herbaceous plants, (b) genera richness of woody and herbaceous plants, and (c) gymnosperms and angiosperms of seed plants.

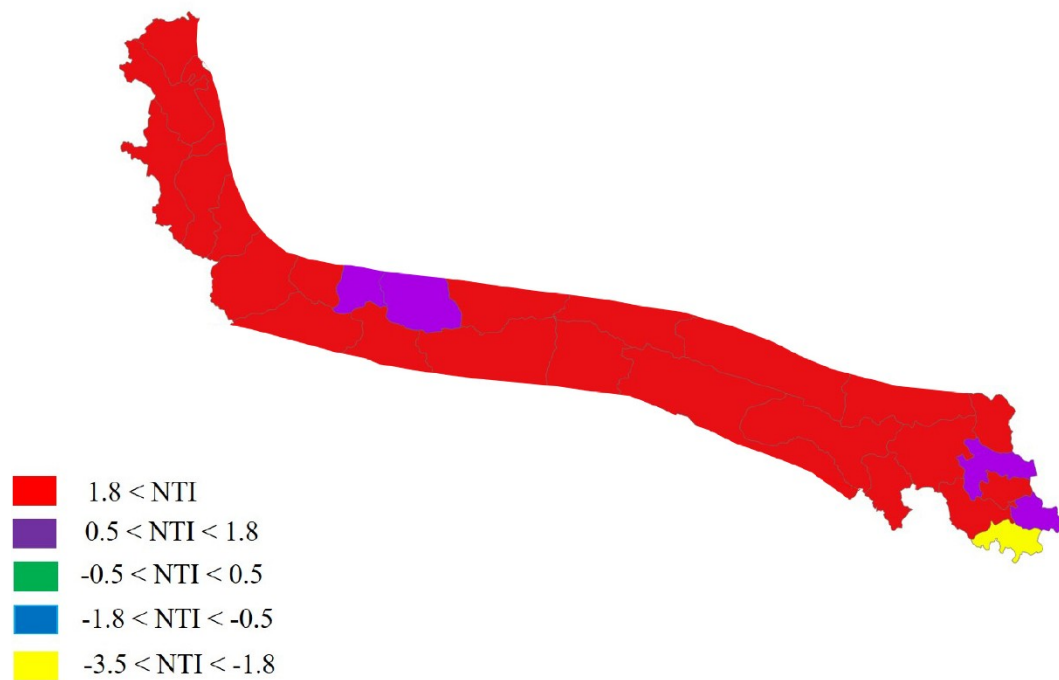


FIGURE 4 Patterns of nearest taxon index (NTI) at the county-level geographical units of the Kunlun Mountains.

