

Both species recolonization and habitat filtering drive the current plant community in temperate region mountains

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Abstract

Biodiversity and community assembly are central topics in ecological studies, and mountains present natural laboratories for studying these issues. Most previous studies have focused on biodiversity hotspots and tropical regions, and relevant research in the middle and high latitudes is relatively limited. We hypothesized that species dispersion and habitat filtering simultaneously might drive the assembly of the current plant community in temperate region mountains. We studied the plant community of the Kunlun Mountains, an independent physical geographic unit located in northwest China on the northern edge of the Qinghai-Tibetan Plateau. We integrated measures of species distribution, geological history, and phylogeography, and analyzed the taxonomic richness, phylogenetic diversity, and phylogenetic community structure of the current plant community in the area. The distribution patterns of 1,911 seed plants showed that species were distributed mainly in the eastern and the southeastern parts of the Kunlun Mountains, which were considered as conservation targets for biodiversity. Similarities of genera and species strongly indicated that mass species migrations exist among the Kunlun Mountains and adjacent biodiversity hotspots. This indicated that the current patterns of species diversity were from species recolonization, and the plant species of the Kunlun Mountains originated primarily from the Hengduan Mountains which are a biodiversity hotspot. The net relatedness index (NRI) indicated that 17 of the 28 communities were phylogenetic clustering, and the others were phylogenetic dispersion. The nearest taxon index (NTI) indicated that 27 of the 28 communities were phylogenetic clustering, and the phylogenetic community structure of Banma County was the only example of overdispersion. By combining the standard effect size phylogenetic diversity (SES-PD) with the two indexes, we showed that species recolonization was likely to be an important evolutionary process affecting the assembly of current plant communities, and that habitat filtering may have drove the ecological processes of these communities.

1 | INTRODUCTION

Understanding biodiversity and community assembly has long been a major interest for ecologists (Grierson et al., 2011; Ma, 2017; Patino et al., 2017). Numerous hypotheses have been proposed to explain these phenomena. The biodiversity hypotheses can be divided into two key categories. Some researchers think that contemporary environmental factors, for instance, climate and habitat heterogeneity, dominate the current mechanisms mediating biodiversity (Kerr & Packer, 1997; Brown, Gillooly, Allen, Savage, & West, 2004; Currie et al., 2004; Wang, Brown, Tang, & Fang, 2009). Others hypothesize that historical processes, such as speciation, extinction, and dispersal, predominantly influence biodiversity (Zobel, 1997; Ricklefs, 2005; Mittelbach et al., 2007). To date, there is no universal theory that integrates the relative influences of contemporary environments and historical processes on biodiversity patterns, even though it is widely accepted that they jointly influence biodiversity (Hawkins & Porter, 2003; Svenning & Skov, 2005, 2007; Montoya, Rodríguez, Zavala, & Hawkins, 2007; Wang, Fang, Tang, & Lin, 2012). In addition, it is a challenge to distinguish the effects of historical processes from those of contemporary environments because of collinearity.

For more than a century, ecologists have proposed numerous hypotheses to explain community assembly. Currently, niche theory (Hutchinson, 1959; Vandermeer, 1972; Silvertown, 2004) and neutral theory (Bell, 2000; Hubbell, 2005) are widely recognized. The former theory argues that species have different niches, while the latter acknowledges that different species within an ecological community can have equivalent ecological functions. Habitat filtering and competition exclusion are principal community assembly rules in niche theory; these are opposing forces that jointly promote community assembly and maintain biodiversity (Webb, Ackerly, McPeck, & Donoghue, 2002). In the neutral theory, the process of community assembly is modeled as being random (Hubbell, 2001). In recent years, ecologists have increasingly recognized that niche and neutral processes are not diametrically opposed and that they are both involved in community assembly (Tilman, 2004; Chase, 2005; Gravel, Canham, Beaudet, & Messier, 2006; Leibold & McPeck, 2006). Rapid advancements in molecular biology, phylogeography, and phylogeny studies, may offer novel insights into community assembly processes. Therefore, ecologists are using these technologies and methods to explain the evolutionary and ecological processes of community assembly over time and at different spatial scales (Faith, 1992; Webb, Ackerly, McPeck, & Donoghue, 2002).

Mountains are topographically complex regions that affect biodiversity and neighboring lowland ecosystem processes by facilitating biotic interchange, influencing regional climate and nutrient runoff (Rahbek et al., 2019a). They offer natural laboratories for studying the mechanisms that govern biodiversity and community assembly. Mountains reportedly influence global terrestrial biodiversity disproportionately, particularly in the tropics, where they host hotspots with extraordinary levels of richness. In the arctic and temperate regions, however, mountain regions host few endemic species and typically have low levels of species diversity, which barely exceed those of the adjacent lowlands (Rahbek et al., 2019b).

The mountains in China are distributed mainly on the Qinghai-Tibetan Plateau (QTP) and in adjacent regions (Wang, Wang, & Fang, 2004). The QTP is the highest and most expansive plateau on the globe, occupying an area of 2.5 million km² with an average elevation over 4,000 m (Zhang, Li, & Zheng, 2002). Extensive research has been conducted on the QTP and the accumulated datasets offer opportunities to investigate the relationship between biodiversity and community assembly in such regions. After the Pleistocene, the QTP experienced four major glacial events (Shi, Li, & Li, 1998; Zhang, Li, & Zheng, 2002; Yi, Cui, & Xiong, 2005), including the Largest Glaciation, which occurred 1.2–0.6 Ma (Liu, Duan, Hao, Ge, & Sun, 2014), when parts of the QTP were entirely covered by ice sheets (Shi, Li, & Li, 1998; Owen, Caffee, Finkel, & Seong, 2008). Such geological processes have driven radiation and species diversification in various groups of plants (Wen, Zhang, Nie, Zhong, & Sun, 2014). According to 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 levels of species richness (Mao et al., 2013).

Several studies have determined the geographical distribution of species in the QTP (Wu, 2008; APGIV, 2016), but the complex environment suggests that species richness would vary considerably across the region (Tang et al., 2006; Yang, Ma, & Kreft, 2013). Due to major advancements in phylogeography studies and tools, the evolutionary histories and underlying adaptations of plants in the QTP have become increasingly clear (Liu, Duan, Hao, Ge, & Sun, 2014), including *Ligularia -Cremanthodium -Parasenecio* (Liu, Wang, Wang, Hideaki, & Abbott, 2006), *Nannoglottis* (Liu, Gao, Chen, & Lu, 2002), *Saussurea* (Wang, Brown, Tang, & Fang, 2009), *Rheum* (Sun, Wang, Wan, Wang, & Liu, 2012), *Gentiana* (Favre et al., 2016), and *Rhodiola* (Zhang, Meng, Allen, Wen, & Rao, 2014), and others (Qiu, Fu, & Comes, 2011; Liu, Luo, Li, & Gao, 2017). Chinese botanists have now completed the construction of the phylogenetic tree for Chinese vascular plants (Chen et al., 2016; Lu et al., 2018), and such datasets facilitate our understanding of plant community of the QTP. Rapid speciation and habitat filtering have been reported to dominate 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). A study revealed that the current flora in the Hengduan Mountains exhibited rapid speciation (Xing & Ree, 2017). Therefore, datasets from different regions provide the opportunity to explore the biodiversity and community assembly in plant communities of different areas.

In the study, we hypothesized that the current plant community in temperate region mountains might be simultaneously driven by species dispersion and habitat filtering. In order to test the hypothesis, the Kunlun Mountains were used as the region of study. These mountains form an independent physical geographical unit with a relatively clear geological history, geographic range, and plant distribution data; however, they are not a biodiversity hotspot (Su, 1998; Zheng, 1999; Pan, 2000; Zachos & Habel, 2011; Wu, 2012–2015; Sun et al., 2015). Thus, they formed a relatively typical temperate mountain chain where we could study plant communities. We used datasets from the Kunlun Mountains region to explore the spatio-temporal patterns of current plant community assembly in this area to: 1) clarify how the plant diversity in the Kunlun Mountains emerged, 2) determine the driving forces of community assembly, and 3) examine the above-mentioned hypotheses with reference to the current plant community assembly in the Kunlun Mountains. An improved understanding of the plant diversity patterns between different regions will help develop better biodiversity conservation strategies.

2 | MATERIALS AND METHODS

| Study area

The Kunlun Mountains are an independent physical geographic unit, 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 northwest Tibet Autonomous Region to the south. The Kunlun Mountains range is oriented east-west, located between 34degN–40degN and 75degE–100degE, with an average altitude >4,000 meters. The range extends for a total length of ~2,500 km and width of 130–200 km. The mountain range is narrower in the west compared to the east and covers a total area of more than 500,000 km² (Zheng, 1999; 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. The area has an annual precipitation that varies from ~100 to 500 mm and an average annual temperature of < 0. The annual precipitation and temperatures show an obvious 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).

The formation of the Kunlun Mountains coincided with the Himalayan movement. According to numerous studies, extensive uplifts of the QTP occurred ca. 15–13 Ma and ca. 8–7 Ma, and the last abrupt and rapid uplift took place 3.6–1.2 Ma (Harrison, Copeland, Kidd, & Yin, 1992; Li, Shi, & Li, 1995; Shi, Li, & Li, 1998; Sun & Zheng, 1998; Spicer et al., 2003). Recent studies have demonstrated that the current QTP ecosystem began in the early Miocene (Deng, Wu, Wang, Su, & Zhou, 2019), and that the Kunlun Mountains reached their present height over the last 17 million years (Pan, 2000; Sun et al., 2015). After the early Miocene, the Kunlun Mountains experienced the Kunhuang movement (Cui et al., 1998) and numerous glacial events (Su, 1998).

To accurately reveal the current plant community, the study region was divided into 28 county-level geographical units. Geographically, the Kunlun Mountains are divided into three parts: east, west, and middle. The western part consists of 6 counties; the middle part consists of 14 counties, with 6 counties on the southern slope and 8 counties on the northern slope; and the eastern part consists of 8 counties.

| Distribution data

The basic distribution data were obtained from *Flora Kunlunica* published in four volumes by Wu and his colleagues (Wu, 2012–2015), with reference 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), and *The Vascular Plants and Their Eco-geographical Distribution of the Qinghai-Tibet Plateau* (Wu, 2008). Based on these sources, and using the order of families from the Angiosperm Phylogeny Group

IV (APGIV, 2016), species were classified into genera and families according to *A Dictionary of the Families and Genera of Chinese Vascular Plants* (Li, Chen, Wang, & Lu, 2018), <http://www.catalogueoflife.org/annual-checklist/2019/>, and <http://www.theplantlist.org>. Genera and species that were not native to the Kunlun Mountains were excluded, and the infraspecific taxa were preserved.

The information presented a comprehensive checklist of the seed plant species in the Kunlun Mountains. To analyze the spatial patterns, these species were divided into 28 county-level geographical units based on species distribution data.

| Similarity of taxa

To determine the origin of the Kunlun Mountains flora (KMF), the species were compared with the flora in nearby biodiversity hotspots. Three biodiversity hotspots exist around the Kunlun Mountains, including the Mountains of Central Asia, the Eastern Himalayas, and the Mountains of Southwest China, which are located to the north, south, and southeast of the Kunlun Mountains, respectively (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Zachos & Habel, 2011). The Mountains of Southwest China host the highest number of plant species among these three biodiversity hotspots, and the Hengduan Mountains are representative of the Mountains of Southwest China. Therefore, the Hengduan Mountains form an important biodiversity hotspot, and harbor one of the richest temperate floras in the world, with ~12,000 vascular plants (Boufford, 2014). We evaluated the species-level, genus-level, and family-level similarities between the KMF and the Hengduan Mountains flora (HMF). The plant species richness in the Kunlun Mountains was approximately one sixth of that in the Hengduan Mountains. The taxa similarity (TS) between the KMF and the HMF was calculated as follows:

$$TS = \frac{SR}{TR} \times 100\%$$

where SR represents the number of shared taxa between a KMF sample and the HMF, TR represents the number of taxa in the KMF sample (taxa represent families, genera, or species), and TS is the similarity of taxa between the KMF sample and the HMF.

| Phylogenetic diversity and structure

We calculated the species level phylogenetic diversity (PD), standard effect size phylogenetic diversity (SES-PD), net relatedness index (NRI), and nearest taxon index (NTI) in each county.

PD was the sum of the phylogenetic length of the communities in each sample and was measured based on the approach developed by Faith (1992). SES-PD was calculated by dividing the difference between the observed (PD_{observed}) and expected phylogenetic diversity (PD_{random}) by the standard deviation (s.d.) of the null distribution (s.d.[PD_{random}]) (Rodrigues et al., 2005), as follows:

$$SES - PD = \frac{PD_{\text{observed}} - PD_{\text{random}}}{\text{s.d.}(PD_{\text{random}})}$$

The NRI and NTI were calculated to analyze community phylogenetic structure (clustering or overdispersion), and to examine possible ecological and evolutionary processes within communities (Webb, Ackerly, McPeck, & Donoghue, 2002). The NRI was based on the mean phylogenetic distance (MPD), which is an estimate of the average phylogenetic relatedness between all possible pairs of taxa within a sample. The 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 NRI and NTI values were calculated as follows:

$$NRI = -1 \times \frac{MPD_{\text{observed}} - MPD_{\text{random}}}{\text{s.d.}(MPD_{\text{random}})}$$

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

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

The phylogenetic analyses require a phylogenetic tree of seed plants, the phylogenetic tree was constructed using Phylomatic (<http://phylodiversity.net/phyloomatic/>) with the stored tree in Zanne et al. (2014). The ecological indexes were calculated using R version 3.3.3 (R Core Team, 2017) and *picante* packages (Kembel et al., 2010).

| Statistical analysis

To examine the community assembly processes in the Kunlun Mountains, two key issues were studied: 1) the patterns of species diversity in the area, and 2) relevant mechanisms relating to community assembly. The HMF has been assembled through recent *in situ* diversification during its rapid uplift over the last 8 Ma (Xing & Ree, 2017). In the northern hemisphere, it is the largest refuge for species in the glacial age (Liu, Luo, Li, & Gao, 2017), and a center for species diversification for many current plants (Wen, Zhang, Nie, Zhong, & Sun, 2014; Chen, Deng, Zhou, & Sun, 2018), such as *Saussurea*, *Gentiana*, *Pedicularis*, *Salix*, *Primula*, *Saxifraga*, *Ranunculus*, and *Corydalis*. Endemic species of seed plants account for 32.4% of the total species in the Hengduan Mountains (Zhang, Boufford, Ree, & Sun, 2009). Therefore, the results of the TS revealed the relationship of species migrations between the Kunlun Mountains and the Hengduan Mountains. The analysis of these results, the geological history, and rules of species migration revealed the patterns of species diversity.

PD and SES-PD have been used to determine the floristic histories of communities (Faith, 1992; Rodrigues et al., 2005). Negative SES-PD values imply that the actual PD is lower than the predicted PD, and the community consists of young flora with relatively close phylogenetic relationships among species; whereas positive SES-PD values imply that the actual PD is higher than the predicted PD, and the community consists of ancient flora with more distant phylogenetic relationships among species. The NRI primarily reflects the structure in deeper parts of a phylogeny and is more appropriate for explaining evolutionary processes; whereas the NTI reflects the structure in shallower parts of a phylogeny, and is more appropriate for exploring ecological processes (Webb, Ackerly, McPeck, & Donoghue, 2002). At the community level, positive NRI and NTI values indicate phylogenetic clustering, whereas negative values indicate phylogenetic dispersion. The analysis of NRIs, NTIs, and SES-PDs were used to explain the evolutionary and ecological processes of community assembly.

3 | RESULTS

3.1 | Richness of taxa

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

At the species level, the seed plants of the KMF comprised 226 woody plants and 1,685 herbaceous plants, accounting for 11.83% and 88.17% of the total species, respectively (Figure 2a). Specifically, the woody plants were represented by 22 trees, 197 shrubs, and 7 lianas; and the herbaceous plants were represented by 9 herbaceous climbers, 224 annual herbs, and 1,452 perennial herbs. There were 570 species endemic to China, accounting for 29.83% of the total, including 81 woody plants and 489 herbaceous plants.

At the genus level, the KMF seed plants were characterized by 39 woody genera, 347 herbaceous genera, and 11 genera that consists of both woody and herbaceous species (Figure 2b). Overall, 7 of these genera (all herbaceous genera) were endemic to the Kunlun Mountains, of which 6 were only distributed in the eastern section. About a third of the plant species were limited to 15 genera, which consisted of more than 20 species in each genus, and there were 155 genera where each genus contained only one species.

From the perspective of vegetation type, the KMF had a relatively low species diversity, with meadows being the primary type, followed by shrubs and grasslands; there were very few forests. Therefore, the biodiversity of KMF varied spatially, with the middle parts of the Kunlun Mountains having the lowest biodiversity, and the forests having the highest biodiversity.

3.2 | Similarity of taxa

The TS between the KMF and the HMF was 55.89% at the species level and 83.38% at the genus level. Nitrariaceae which was only distributed in 10 counties was not found in the Hengduan Mountain, and the minimum TS was 96.88% at the family level. Therefore, family level TS estimates had little value for further assessing patterns in biodiversity. The TS of woody species and herbaceous species were 57.52% and 55.67%, respectively. According to the endemic taxa data, the TS of endemic species was 70%, and the endemic genera in the Kunlun Mountains were also found in the Hengduan Mountains. The TS of woody genera and herbaceous genera were 82.05% and 83.86%, respectively, while the TS of genera with both woody and herbaceous species was 72.73%.

In the 28 county-level geographical units, the TS of the counties decreased from the east to the west, and increased from the north to the south (Table 1). At the species level, the maximum TS was 93.86% in Banma County and the minimum was 24.53% in Wuqia County. The TS was higher than 50% in the eastern section, it was 40%–50% in the middle section and was less than 40% in the western section of the Kunlun Mountains (Table 1). At the genus level, 26 counties had TS estimates higher than 80%, and 2 of the 26 counties had TS estimates of 100%, named Banma County and Gande County. The minimum TS was 76.61% in Ruoqiang County, while the TS of Wuqia County was 78.75% (Table 1).

3.3 | Phylogenetic diversity and structure

The TR and PD were higher at both ends of the ranges. The lowest TR and PD values were observed in Minfeng County, and the values in the eastern area were higher than those in the western area (Table 2).

In the present study, only one SES-PD value was greater than 0, and all other SES-PD values were less than 0. The maximum and minimum SES-PDs were 3.56 and -5.69, respectively (Table 2). The negative SES-PD values indicated that 27 of the 28 county-level communities were young flora, while the positive SES-PD value for the Banma County indicated that the flora there were relatively ancient. No significant differences were observed in the SES-PDs between Jiuzhi County and Shache County, whereas significant differences were detected among the other SES-PD values ($P < 0.05$) (Table 2).

Phylogenetic structure can be revealed by the NRI and NTI. These indexes indicated that the different counties had different phylogenetic structures (Figures 3, 4). Negative NRIs in 11 county-level communities indicated phylogenetic dispersion. These counties were located mainly in the western and middle parts of the Kunlun Mountains. Conversely, positive NRIs in the 17 other county-level communities indicated phylogenetic clustering. These counties were distributed mainly in the eastern and middle parts of the Kunlun Mountains. Significant differences were detected between four negative NRIs ($P < 0.05$) and three positive NRIs ($P < 0.05$), while the NRIs of the remaining 21 counties were not significant (Figure 3). In addition, the NTIs of 27 county-level communities were positive, of which 24 NTIs were statistically significant ($P < 0.05$). Only the community in Banma County had a negative NTI that was also significantly different ($P < 0.05$) (Figure 4). However, inconsistent trends were observed between the NRIs and NTIs in 10 counties, most of which bordered the Qaidam and Tarim Basins (Figures 3, 4).

Overall, both the NRI and NTI values were negative in the Banma County. The other 27 counties had positive NTI values, 17 of which also had positive NRI values. Ten counties had negative NRI values and

were adjacent to the Qaidam and Tarim Basins (Figures 3, 4).

4 | DISCUSSION

4.1 | The patterns of species diversity

Overall, there were difference in the species distribution between the Kunlun Mountains and the Hengduan Mountains: 55.89% of the species in the Kunlun Mountains occurred in both the Kunlun Mountains and the Hengduan Mountains, and the level of similarity was higher than 80% at the genus level. Similar patterns were observed in the endemic taxa, where 70% of the endemic species in the Kunlun Mountains were also distributed in the Hengduan Mountains; all the endemic genera in the Kunlun Mountains were found in the Hengduan Mountains. The TS declined across the 28 county-level geographical units with an increase in distance from the Hengduan Mountains (Table 1). Therefore, our study strongly indicated that mass species migrations occurred between the KMF and the HMF at both the genus and species levels.

Some studies have suggested that the diversity hotspots of Chinese endemic seed flora are in the Qinling Mountains and further south, or in the Hengduan Mountains and to the east of China (Huang et al., 2016). Similar rules exist regarding the hotspots of endemic woody seed plants in China (Huang et al., 2012). Around 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). The Kunlun Mountains were not a hotspot of Chinese endemic seed flora or a center of diversification for current plants. However, endemic species of seed plants accounted for 29.8% of the total species in the Kunlun Mountains. The proportion of endemic species of the Kunlun Mountains was higher than that of QTP, and lower than that of the Hengduan Mountains. Consequently, these endemic species in the Kunlun Mountains may have come from the current speciation centers. The results of SES-PDs also indicated that the KMF is relatively young flora (Table 2) and that the young flora may have come from the speciation centers.

The Kunlun Mountains reached their present altitude over the last 17 million years (Sun et al., 2015), during which they experienced dramatic climatic fluctuations (Deng, Wu, Wang, Su, & Zhou, 2019) and geological movements (Cui et al., 1998). The climatic conditions have changed from hot and humid to cold and dry (Zheng, 1999). In addition, since the Pleistocene, the region has experienced numerous glacial events (Su, 1998), for example, the Largest Glaciation (1.2–0.6 Ma) and the Last Glacial Maximum (Shi, Zheng, & Yao, 1997). In the Last Glacial Maximum, the Kunlun Mountains were mostly covered by a unified ice sheet (Shi, Zheng, & Yao, 1997; Su, 1998). These numerous glaciations have led to mass extinction events in the Kunlun Mountains. Many plant molecular phylogeography studies have reported that the QTP was recolonized by most current plants in the postglacial period, from the southern or eastern glacial refugia (Wiens & Donoghue, 2004; Qiu, Fu, & Comes, 2011; Yu & Zhang, 2013; Yan & Tang, 2019). Some hardy plants also persisted in micro-glacial refugia and dispersed into adjacent regions in the postglacial period. Consequently, after these glacial events, the current plants may have originated from refuges adjacent to the Kunlun Mountains.

The findings of the present study improve our understanding of the patterns of species diversity in the Kunlun Mountains. First, the KMF were tightly linked with the HMF at both the species and genera levels. Second, after numerous glacial events, it is probable that the current plants originated from adjacent refuges. The PD and SES-PD of the KMF also supported the conclusion that the current plants may have originated from a diversification center. The endemic species provided further evidence that they may have come from the current speciation centers. Third, previous studies revealed that the primary direction of species migration is from east to west or from south to north during the interglacial periods in the QTP and adjacent areas (Qiu, Fu, & Comes, 2011; Yu & Zhang, 2013; Yan & Tang, 2019). Fourth, The Hengduan Mountains have been confirmed as the largest refuge for species in the glacial periods (Liu, Luo, Li, & Gao, 2017), a center of species diversification for many current plants (Wen, Zhang, Nie, Zhong, & Sun, 2014; Chen, Deng, Zhou, & Sun, 2018), and a hotspot for Chinese endemic seed flora (Huang et al., 2016). Therefore, the above findings revealed that species recolonization underpinned the current patterns of species diversity in the

Kunlun Mountains, and that the KMF originated primarily from the HMF.

4.2 | Processes of community assembly

Community assembly occurs via the combined influence of evolutionary and ecological processes. Whereas evolutionary processes relate to the origins of species, such as speciation and extinction, ecological processes address how species are assembled, for example, via habitat filtering or competition exclusion. With rapid advances in molecular biology, the phylogenetic structures of communities can be better assessed (Faith, 1992; Webb, Ackerly, McPeck, & Donoghue, 2002). The analysis of community phylogenetic structure can facilitate the determination of the ecological and evolutionary processes that regulate community assembly at different scales (Webb, Ackerly, McPeck, & Donoghue, 2002). Evolutionary processes such as rapid *in situ* speciation, niche conservatism, and dispersal limitation can lead to phylogenetic clustering (Lu et al., 2018). In comparison, evolutionary processes such as niche evolution, convergent evolution, and colonization may lead to phylogenetic overdispersion within communities (Allen & Gillooly, 2006). For ecological processes, habitat filtering and competition exclusion can result in non-random community phylogenetic structures (Webb, Ackerly, McPeck, & Donoghue, 2002). Habitat filtering which can lead to phylogenetic clustering refers to the selection of certain traits of species in a community (Wiens & Graham, 2005), whereas competition exclusion can result in phylogenetic dispersion (Burns & Strauss, 2011).

Overall, the SES-PD results illustrated the floristic history of the counties; 27 county-level communities had young flora, while only one county-level community contained ancient flora (Banma County). Therefore, the TR, PD, and SES-PD results suggested that the eastern parts of the Kunlun Mountains were the center for biodiversity conservation; and that the KMF was comprised primarily of young flora, which was consistent with the findings of a previous study (Lu et al., 2018).

In the western and the middle parts of the Kunlun Mountains, the negative NRIs in 10 county-level communities indicated that these communities were the result of phylogenetic dispersion, however, significant differences were observed in only three negative NRIs ($P < 0.05$), whereas the other negative NRIs had no significant differences. The positive NRIs in 10 county-level communities indicated that these communities showed phylogenetic clustering, however, these positive NRIs were not significantly different. The positive NTIs in 20 county-level communities indicated that these communities were phylogenetic clustering, however, two NTIs were no significant differences, whereas the remaining NTIs did show significant differences ($P < 0.05$).

In the eastern parts of the Kunlun Mountains, the NRI and NTI of Banma County were negative, and the two indexes were statistically significant ($P < 0.05$). The result suggested that the community in Banma County was phylogenetic overdispersion. The NRI and NTI of other counties were positive which indicated that these communities were phylogenetic clustering, however, significant differences were detected between three NRIs ($P < 0.05$) and six NTIs ($P < 0.05$).

NRI and NTI analyses can help to reveal the ecological and evolutionary processes in a community. First, the latest research shows that China is identified as having five phytogeographical regions, including the Paleotropic, Holartic, East Asiatic, and Tethyan regions, as well as the QTP. The relationships among the regions have been inferred as follows: (Paleotropic [East Asiatic + Holarctic] + [Tethyan + QTP]) (Ye et al., 2019). The Kunlun Mountains are in the transition zone between the Tethyan region and the QTP. Therefore, the current plants of the Kunlun Mountains may have originated from multiple phytogeographical regions. Second, the current environment in the Kunlun Mountains is dry and cold, particularly in the western and middle parts (Zheng, 1999). In addition, both the Qaidam and the Tarim Basins belong to the Tethyan region (Ye et al., 2019), and they are contiguous with the Kunlun Mountains. The plants that are well adapted to drought stress and cold conditions may have originated from the Tethyan regions and alpine flora of other regions. However, the phylogenetic relationships among the species are distant, because they may have originated from different phytogeographical regions. Third, the mechanisms driving biodiversity patterns after glacial events are the expansion of seed plants from adjacent glacial refugia into the Kunlun Mountains.

In the western and the middle parts of the Kunlun Mountains, the negative NRIs in 10 county-level communities may indicate that the current species were from multiple phytogeographical regions, named the Tethyan regions and the alpine flora of the Hengduan Mountains according to geographical location. The positive NRIs in the 10 county-level communities indicated that most of the species were from relatively homogeneous phytogeographical regions, for example, the species in the western parts may have mainly originated from Mountains of Central Asia, the species on the northern slopes of the middle parts may have mainly originated from the Tethyan regions, and the species on the southern slopes of the middle parts may have mainly originated from the alpine flora of the Hengduan Mountains. Therefore, recolonization of species from different phytogeographical regions may have dominated the evolutionary processes of the current communities in the 20 county-level communities. The NTI values were positive in 20 counties, which indicated that habitat filtering presented a strong explanation for the ecological processes of communities in the western and middle parts of the Kunlun Mountains.

In the eastern parts of the Kunlun Mountains, the NRI and NTI of Banma County were negative, which suggested that the community in Banma County results from species that originated from the alpine flora and forest flora of the Hengduan Mountains. The positive NRI and NTI values in seven county-level communities indicated that the species in these communities originated from the alpine flora of the Hengduan Mountains, and that the environmental conditions in the area selected for species possessing similar traits.

In conclusion, both species recolonization and habitat filtering may contribute to current plant communities of the Kunlun Mountains via ecological and evolutionary processes, and habitat filtering may play a critical role in an ecological processes.

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Data Accessibility

Data are available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2ngf1vhk3>

Competing Interests

None declared.

Author Contributions

Du Weibo collected basic data, organized data, posed scientific question and wrote manuscripts; Jia Peng calculated the species level phylogenetic diversity (PD), standard effect size phylogenetic diversity (SES-PD), net relatedness index (NRI), and nearest taxon index (NTI) in each county; this article was guided by Du Guozhen.

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Tables

TABLE 1 Taxa similarity (TS) of 28 counties in the Kunlun Mountains.

East Kunlun Mountains	East Kunlun Mountains	East Kunlun Mountains
Counties	Species TS	Genera TS
Banma	93.86%	100%
Jiuzhi	91.23%	99.48%
Dari	84.03%	99.15%
Gande	88.24%	100%
Chenduo	83.47%	97.22%
Maduo	72.19%	95.04%
Maqin	81.98%	97.05%
Xinghai	76.27%	92.02%
South slope of Middle Kunlun Mountains	South slope of Middle Kunlun Mountains	South slope of Middle Kunlun Mountains
Counties	Species TS	Genera TS
Qumalai	78.61%	96.50%
Zhiduo	70.99%	97.40%
Bange	57.36%	90.14%
Nima	51.38%	93.75%
Gaize	54.39%	85.07%
Ritu	54.37%	86.72%

TABLE 2 Taxonomic richness (TR), phylogenetic diversity (PD), and standard effect size phylogenetic diversity (SES-PD) of seed plants among county-level geographical units of the Kunlun Mountains.

East Kunlun Mountains	East Kunlun Mountains	East Kunlun Mountains
Counties	TR	PD
Banma	391	19934.01
Jiuzhi	536	22661.04
Dari	288	12746.95
Gande	153	8040.96
Chenduo	489	19732.64
Maduo	470	17770.41
Maqin	748	29302.68
Xinghai	731	27205.84
South slope of Middle Kunlun Mountains	South slope of Middle Kunlun Mountains	South slope of Middle Kunlun Mountains
Counties	TR	PD
Qumalai	359	14850.76
Zhiduo	162	8626.90
Bange	128	7309.88
Nima	109	5919.10
Gaize	114	6061.40
Ritu	263	11778.09

Figure legends

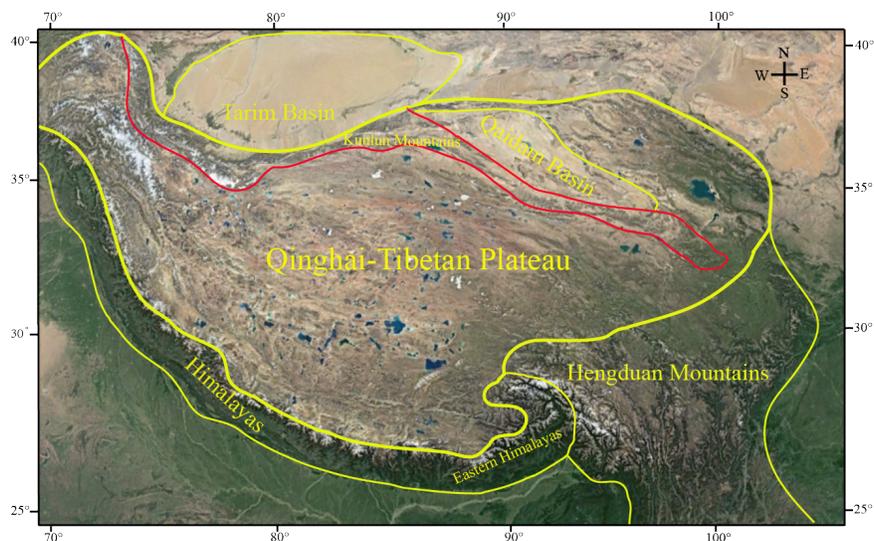


FIGURE 1 Geographical location of the Kunlun Mountains (outlined in red).

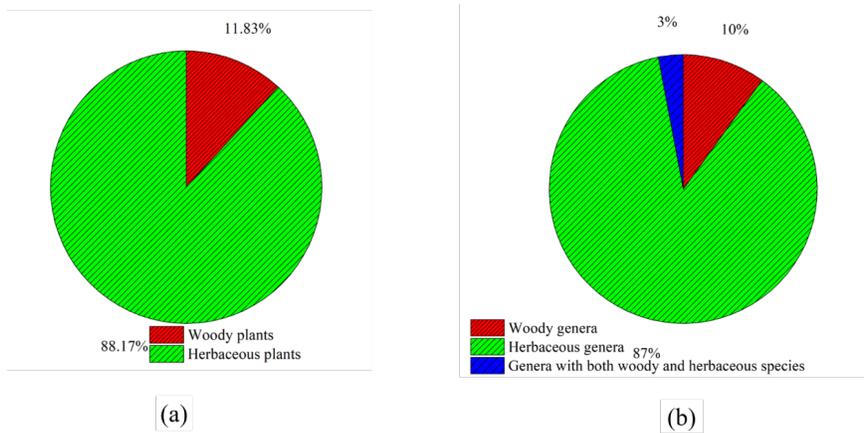


FIGURE 2 Taxa richness of woody and herbaceous plants in the Kunlun Mountains. (a) Species richness and (b) genera richness of woody and herbaceous plants.

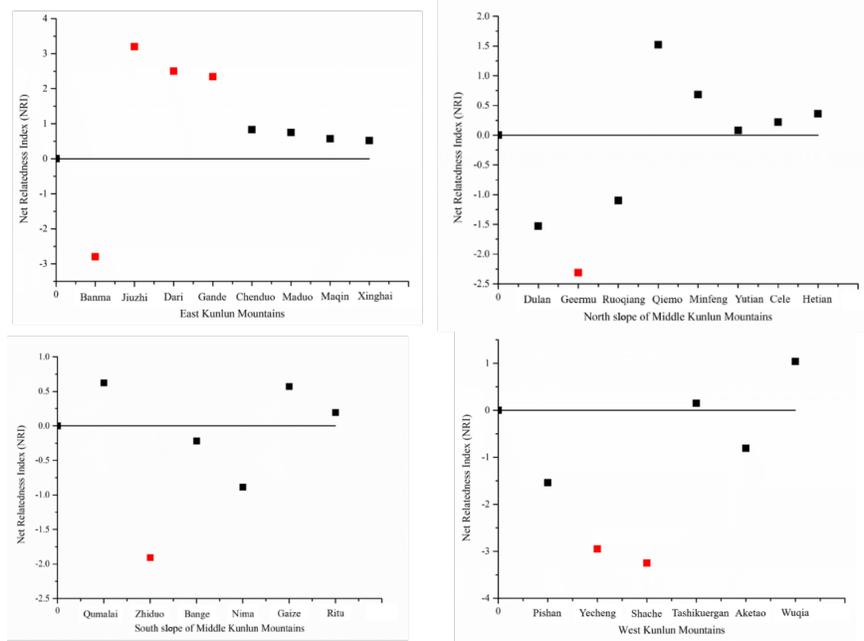


FIGURE 3 County-level net relatedness index (NRI) of the Kunlun Mountains. Values with $P < 0.05$ are depicted as red squares, and values with $0.95 < P < 0.05$ are depicted as black squares.

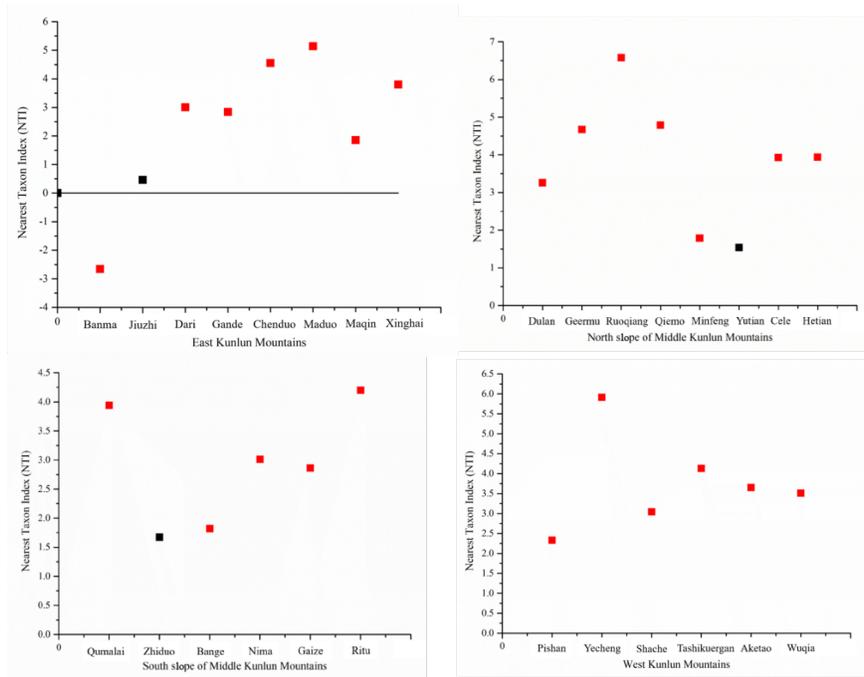
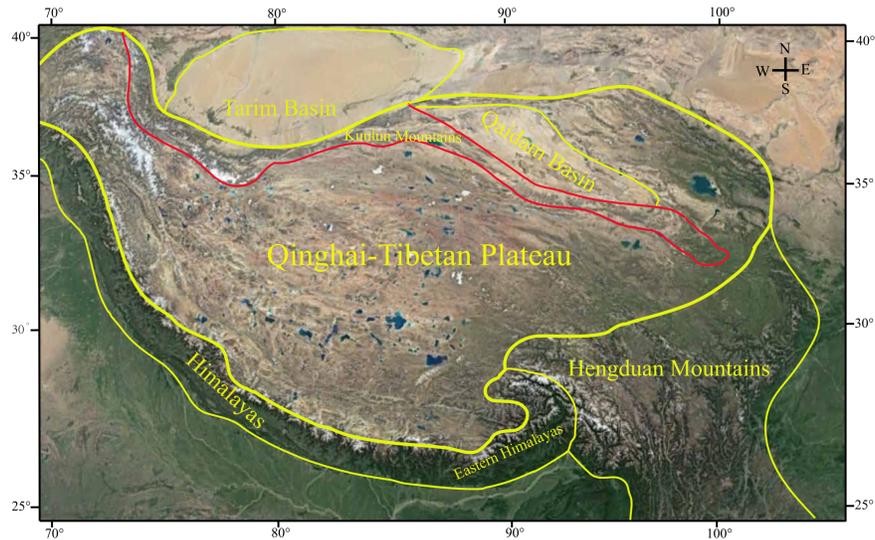
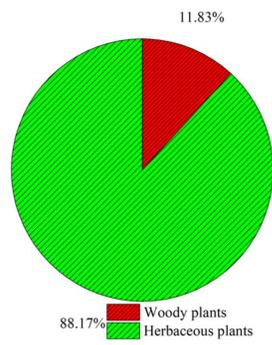


FIGURE 4 County-level nearest taxon index (NTI) of the Kunlun Mountains. Values with $P < 0.05$ are depicted as red squares, and values with $0.95 \leq P < 0.05$ are depicted as black squares.

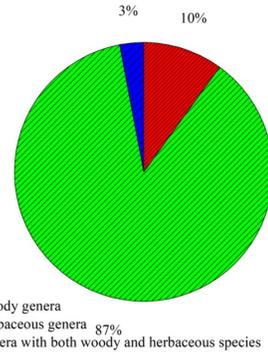
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Tables.docx available at <https://authorea.com/users/312339/articles/442930-both-species-recolonization-and-habitat-filtering-drive-the-current-plant-community-in-temperate-region-mountains>





(a)



(b)

