

Testing multiple hypotheses for the high endemic plant diversity of the Tibetan Plateau

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Abstract

Aim: The Tibetan Plateau harbours the highest alpine and endemic plant diversity in the world, attributed to rapid diversification during the plateau uplift and Quaternary climate fluctuations. However, there is little understanding of which hypotheses associated with these geological and climatic processes garner strong support as explanations for the observed diversity patterns. Here, we test support for hypotheses related to uplift and climate changes that could account for the high endemism and phylogenetic diversity of the world's highest plateau.

Location: Tibetan Plateau (TP).

Time period: Neogene, Quaternary and current period.

Major taxa studied: Tibetan endemic seed plants.

Methods: We collated data on endemic seed-plant distribution based on county-level mapping from published monographs and online databases. We calculated species richness (SR) and phylogenetic diversity for endemic herbs, shrubs, trees, and all plants for 0.5-degree × 0.5-degree grid cells covering the TP. We derived environmental and evolutionary predictors to evaluate eight biogeographical hypotheses associated with plateau uplift and climate fluctuations, and used partial regression analysis and mixed conditional autoregressive (CAR) models to assess the relative contribution of each predictor to the extant diversity of the TP.

Results: We found plateau uplift independently explained more variance in diversity than climate fluctuations, but there were also strong interaction effects. The full CAR models including all predictors explained 37%–75% of the total variation across diversity measures and life forms. The predictor representing the montane museum hypothesis explained the most variation (c. 25%), but each predictor explained at least 6%.

Main conclusions: These results demonstrate that both the plateau uplift and Quaternary climate fluctuations had large impacts on current patterns of species diversity, but the influence of plateau uplift was more pronounced than that of climate changes. Our study suggests that plateau uplift and climate changes are the original drivers of complex biogeographical processes accounting for the biodiversity of the TP.

KEYWORDS

alpine plants, biodiversity, climate changes, dispersal, endemism, mountain uplift, Neogene, Quaternary, Tibetan Plateau, vicariance

1 | INTRODUCTION

Mountainous areas are hotspots of biodiversity and endemism, due to their highly varied topography, diverse range of climatic zones, high primary productivity and long-term environmental stability (Hoorn, Mosbrugger, Mulch, & Antonelli, 2013; Körner et al., 2017). Over the long history of biological evolution on Earth, mountain formation, climate change and the interactions between them have profoundly influenced the distribution and diversity of a broad range of organisms (Fjelds , Bowie, & Rahbek, 2012; Mastretta-Yanes, Moreno-Letelier, Pinero, Jorgensen, & Emerson, 2015; Merckx et al., 2015). For example, the uplift of extensive mountain ranges during the Neogene (e.g., the Andes, the Rockies, Hengduan, Himalaya), and subsequent cyclic Quaternary climate fluctuations, triggered the radiation and diversification of numerous cold-adapted species that greatly shaped alpine species diversity (Drummond, Eastwood, Miotto, & Hughes, 2012; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016; Qu et al., 2015). These effects are evident today in several biodiversity hotspots located in montane areas (K rner, 2004; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). However, despite the clear association between the evolution and maintenance of high biodiversity in mountainous regions, little is known about the contribution made by the different mechanisms proposed by the hypotheses to explain it. Such understanding is necessary to inform biodiversity conservation efforts in the face of accelerating global change.

The Tibetan Plateau (TP), the largest mountain formation in the world, harbours a great number of alpine and endemic species (Zhang, Ye, & Sun, 2016). Commencing with the collision of the Indian plate and Eurasian continent around 50 million years ago (Ma), the TP formed from progressive uplift until the Neogene period (Miocene and Pliocene) when rapid and extensive plateau uplift occurred (Deng & Ding, 2015; Li, Shi, & Li, 1995). Subsequent to the uplift, global cooling and periodic Quaternary glaciations drove mountain glaciers of different scales to expand downward and occupy large areas of the TP (Shi, Li, & Li, 1998). Thus, the TP has experienced substantial geological and climatic changes over the past 50 million years, affecting the evolution and diversity of the alpine flora and leading to its exceptionally high endemism (Favre et al., 2015).

Based on lineage divergence times of (sub-)alpine plants in the TP, there is a general consensus that the diversification of genera occurred mainly during the rapid and extensive uplift of the Neogene period (e.g., *Saxifraga*, Ebersbach et al., 2017; *Gentiana*, Favre et al., 2016; *Rhodiola*, Zhang, Meng, Allen, Wen, & Rao, 2014). At the species level, however, the divergence of main clades happened largely during the late Pliocene and Pleistocene (e.g., *Pomatosace filicula*,

Wang, He, Miede, & Mao, 2014; *Bupleurum smithii*, Zhao, Ma, Liang, Wang, & He, 2013). Thus, evidence suggests that plants of the TP may have diversified in response to both the Neogene plateau uplift and the subsequent Quaternary climate fluctuations (Hughes & Atchison, 2015; Lu et al., 2018; Qiu, Fu, & Comes, 2011; Wen, Zhang, Nie, Zhong, & Sun, 2014). However, it is unclear which of the hypotheses associated with these distinct geological and climatic processes garner the strongest support as explanations for the contemporary diversity patterns.

Leading mechanisms proposed by the hypotheses to explain speciation and diversity distribution in the TP can be associated predominantly with Neogene plateau uplift or Quaternary climate fluctuations (Table 1). Hypotheses associated with uplift emphasize the role of environmental change (e.g., topographic and climatic gradients) in forming a diverse range of novel habitat cradles for speciation and diversification. For example, increased topographic heterogeneity could extend any topography-associated niche dimensions (e.g., water availability), allowing more species to coexist (Kerr & Packer, 1997). On the other hand, bioclimatic disparities due to plateau uplift could result in parapatric speciation along the climatic gradients with more species existing within areas of high climatic stratification (Endler, 1982). The montane museum hypothesis (Stebbins, 1974) proposes that species originated under conditions found only at mid-elevations in the current landscape. As species originally found at these mid-elevations have had a longer time to diverge than those at higher and lower elevations, greater diversity occurs at these intermediate elevations (i.e., the "time-for-speciation" effect; Stephens & Wiens, 2003; Vetaas & Grytnes, 2002). Another uplift-based hypothesis invokes the formation of large numbers of geographically isolated areas where the combination of divergent lineages, speciation and adaptive evolution could result in higher diversity (Vandergast, Bohonak, Hathaway, Boys, & Fisher, 2008; Wood et al., 2013).

Hypotheses based on Quaternary climate fluctuations relate to their effects on population demography, dispersal or speciation (Table 1). For example, areas of high climatic stability or refugia during the glacial periods could support speciation and endemism by either providing more time for localized species to become more specialized, or for recolonizing lineages to converge (Dynesius & Jansson, 2000; Vandergast et al., 2008). During the interglacial or post-glacial periods, newly exposed areas could represent a dispersal corridor to facilitate population expansion after glaciation (Chan, Brown, & Yoder, 2011). Periodic glacial-interglacial disturbance cycles could also isolate populations, promoting allopatric divergence (Colinvaux, 1993). In such a case, high species richness (SR) and endemism would be expected in areas experiencing the greatest temperature changes within highlands.

Any combination of these hypotheses could be consistent with observed patterns of plant diversification in the TP during the Neogene, and the continued diversification of some lineages through the Quaternary (see Supporting Information Tables S1, S2 and Figures S1, S2; a list of the data sources is found in the Appendix). However, the relative merits of the various explanatory hypotheses have yet to be directly assessed. In this study, we developed a range of environmental and evolutionary predictors as proxies for eight biogeographical hypotheses associated with diversification presented in Table 1. We used these predictors as explanatory variables to test support for each hypothesis in creating observed patterns of taxonomic and phylogenetic diversity (PD) for a range of life forms for species endemic to the TP. Our aim was to evaluate the relative merits of these competing hypotheses as explanations for the formation and maintenance of plant diversity in alpine regions in general and the TP in particular.

2 | METHODS

2.1 | Study area

The TP is the largest (c. 2.5×10^6 km²) and highest altitude plateau in the world, with an average elevation above 4,000 m (Figure 1). It harbours a diverse alpine flora with high endemism (Zhang et al., 2016). Several major Asian rivers including the Mekong, Salween, Yarlung

Zangbo, Indus and Ganges originate in the TP. During the summer, both the Indian and East Asian monsoons bring warm and wet conditions critical for alpine plant growth and reproduction. Two global biodiversity hotspots (the Hengduan and Himalaya Mountains) in the region are the potential origin pools of many temperate plants (Myers et al., 2000; Wu, 1988).

2.2 | Species data

We selected seed plant species found only in the TP (i.e., endemic species) according to the geographical boundary of the TP (Figure 1; Zhang, Li, & Zheng, 2002). We recorded plant spatial distributions based on county-level mapping from the following monographs: *The Vascular Plants and Their Eco-geographical Distribution of the Qinghai-Tibetan Plateau* (Wu, 2008), *Flora Reipublicae Popularis Sinicae* (Editorial Committee of Flora Reipublicae Popularis Sinicae, 1959–2004), *Flora of China* (Wu, Raven, & Hong, 1994–2013) and *Diversity and Geographical Distributions of Chinese Endemic Seed Plants* (Huang, Ma, & Chen, 2015). For species with no distributional data, we referred to several online databases, including the Chinese Virtual Herbarium (<https://www.cvh.ac.cn/>) and the Global Biodiversity Information Facility (<https://www.gbif.org/>). The preliminary species list was based on the *Flora of China* with any species under a synonym or assigned an incorrect name excluded. Taxonomy followed the APG IV classification (The Angiosperm Phylogeny Group, 2016).

TABLE 1 Major biogeographical hypotheses testing the effects of Neogene plateau uplift and Quaternary climate changes on species diversity in the Tibetan Plateau

Hypothesis	Mechanisms	Predictions	References
<i>Neogene plateau uplift</i>			
Topographic heterogeneity	Niche differentiation or potential geographical barriers invoke allopatric speciation	Areas of high heterogeneity harbour more endemic species	Kerr and Packer (1997)
Montane museum	Habitats of median elevation have more time for speciation and accumulation of species	Areas at mid-elevation possess high species richness and endemism	Stebbins (1974); Stephens and Wiens (2003)
Climatic gradient	Parapatric speciation along the climatic gradient	High species richness and endemism exist within areas of high climatic stratification	Endler (1982)
Geographical isolation	Hybridization when divergent lineages encountered	Divergence hotspots harbour more endemic species	Vandergast et al. (2008); Wood et al. (2013)
<i>Quaternary climate changes</i>			
Climatic stability	Stable climate allows localized species to persist and thus become highly specialized and differentiated	Areas of climatic stability harbour high species richness and endemism	Dynesius and Jansson (2000)
Refugia	Refugia preserve ancient lineages and other recolonized lineages	Refugia usually harbour more species during the glaciation	Vandergast et al. (2008)
Disturbance–vicariance	Temperature fluctuations drive species toward highlands, resulting in allopatric speciation	High species richness and endemism are found in highlands or areas with high temperature variation	Colinvaux (1993)
Dispersal corridor	Suitable areas facilitate species migration in face of climate changes	Areas of high migration harbour more endemic species	Chan et al. (2011)

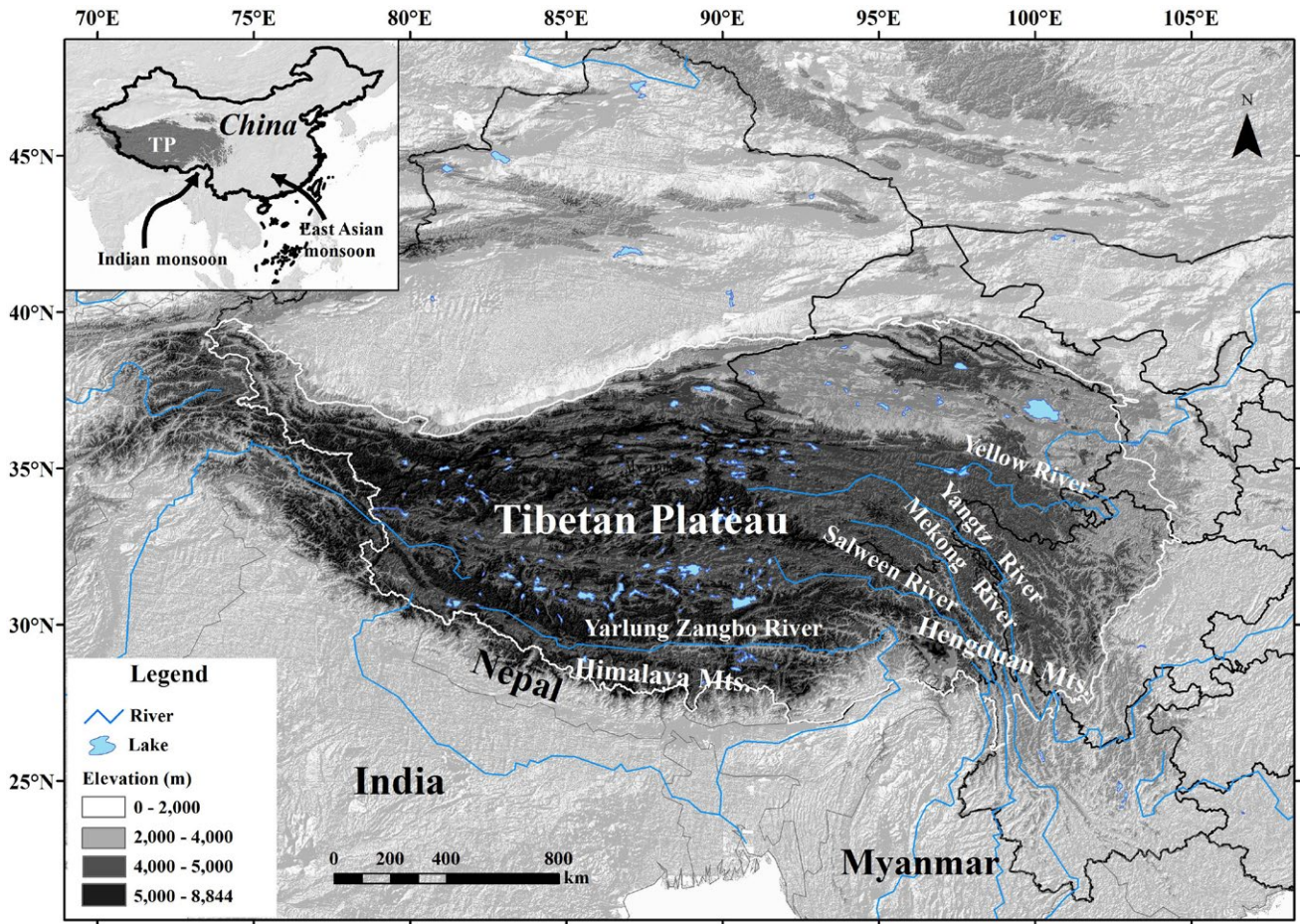


FIGURE 1 Map of the Tibetan Plateau (TP) and its basic geographical features. The TP is the source of several major Asian rivers including the Mekong, Salween, Yarlung Zangbo, Yangtze and Yellow Rivers. Each summer, both the Indian and East Asian monsoons bring warm and wet conditions critical for species growth and reproduction. Two global biodiversity hotspots (the Hengduan and Himalaya Mountains) are located in the southeastern edge of the TP

We converted the county-level distribution of each species into a grid-based map. To do this, we divided the TP into 1,126 grid cells of dimension 0.5-degree × 0.5-degree (approximately 50 km × 50 km). Then, we compared the elevational range of a species' distribution with that of a grid cell. If there was a match, this species would be recorded as present in this grid, otherwise it would be recorded as absent. Finally, we used the grid-based data to build a species presence/absence data matrix.

2.3 | Response variables: Diversity indices

We used two indices to quantify endemic plant diversity: SR and PD. SR is simply the number of Tibetan endemic species in total, and for each life form (tree, shrub and herb) within a spatial unit (grid cell). To quantify PD, we used Faith's (1992) index, which is defined as the total phylogenetic branch length among all taxa in an area. First, we built a phylogenetic tree of all Tibetan endemic species (see Supporting Information Appendix S1) based on the dated phylogeny for Chinese angiosperms. The supertree for Chinese angiosperms was constructed using four plastid genes (*atpB*, *matK*, *ndhF* and *rbcl*),

one mitochondrial gene (*matR*) and 138 fossil calibrations (Chen et al., 2016; Lu et al., 2018). Because this supertree is a genus-level tree from which only one or a few species was sampled for each genus, it requires a species matching process. We put Tibetan endemic species into the DarwinTree datasets (<https://www.darwintree.cn/>) to find their corresponding species in the supertree (see Supporting Information Appendix S2). Then, based on the matching species list, we extracted from the supertree to obtain the dated phylogeny for Tibetan endemic plants using the package Ape (Popescu, Huber, & Paradis, 2012) in R 3.4.4 (R Core Team, 2016). Finally, we used the R package Picante (Kembel et al., 2010) to calculate the PD values for each grid cell. The calculation of PD for distinct life forms (tree, shrub and herb) followed the same process as above. The SR and PD values were logarithm-transformed prior to analysis.

2.4 | Predictors used to test environmental and evolutionary hypotheses

To test support for the different processes in accounting for the endemic species diversity, we calculated eight predictors, each

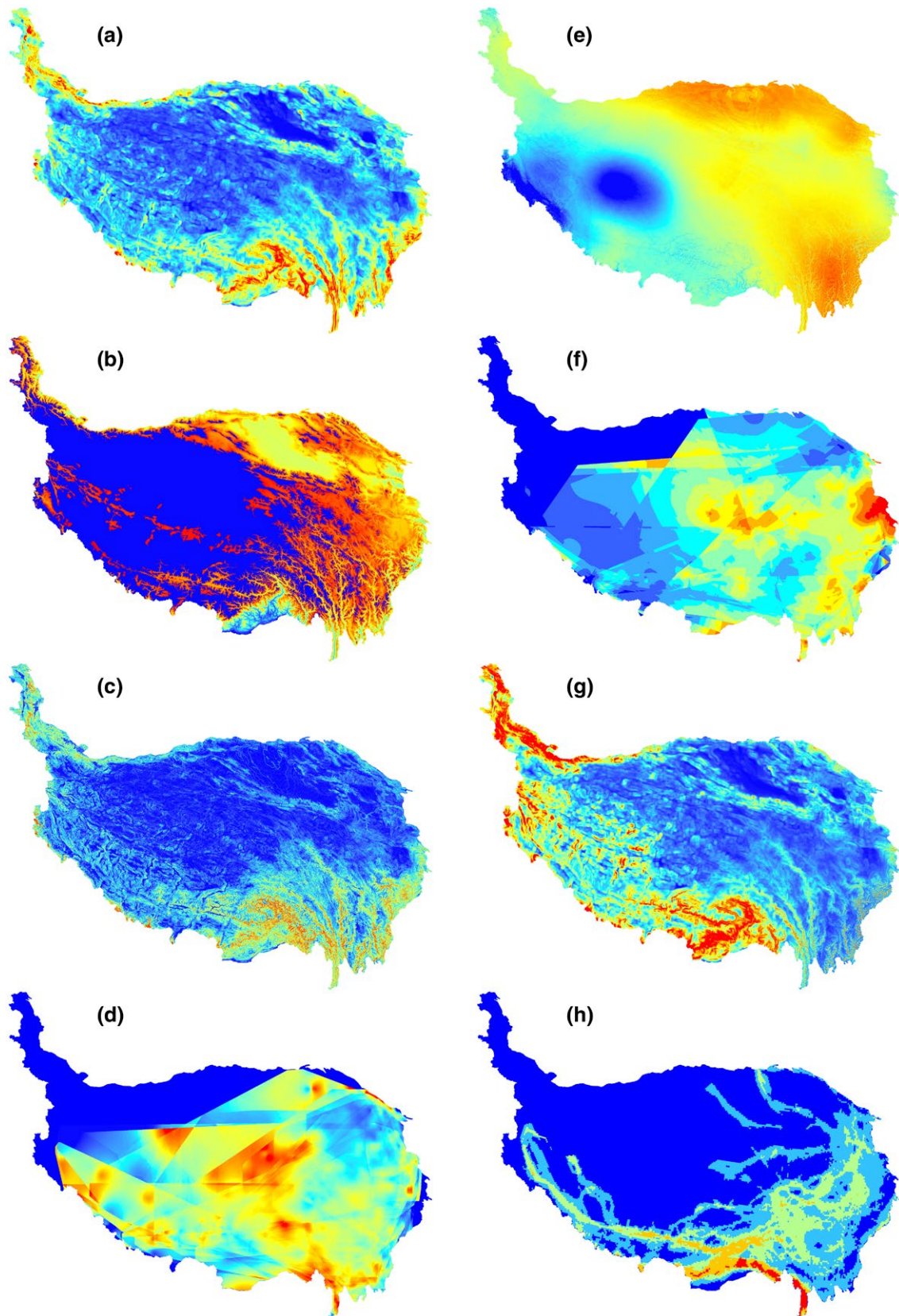


FIGURE 2 Distributions of environmental and evolutionary variables in the Tibetan Plateau. Variables related to the Neogene plateau uplift are (see Table 1): (a) topographic heterogeneity, (b) montane museum, (c) climatic gradient, (d) geographical isolation. Variables related to the Quaternary climate fluctuations are: (e) climatic stability, (f) glacial refugia, (g) vicariance–disturbance and (h) dispersal corridor. Warmer colours indicate higher values in each map

representing a measurable property of hypotheses associated with Neogene plateau uplift or Quaternary climate fluctuations (Table 1). Below we detail the hypothesis represented by each predictor and how it was calculated (summarized in Supporting Information Table S3).

2.4.1 | Hypotheses related to Neogene plateau uplift

Uplifting during the Neogene period dramatically altered the topography of the TP. We tested two hypotheses relating to this (Table 1): *Topographic heterogeneity* (also known as the montane species pump; Kerr & Packer, 1997) and *Montane museum* (time-for-speciation; Stephens & Wiens, 2003). Topographic heterogeneity (Figure 2a) was quantified as the *SD* of elevation within a target cell and the eight neighbouring cells (c. 10 km²) using the SDMT_{TOOLBOX} v. 1.1c (Brown, 2014). To test the montane museum hypothesis (Figure 2b), we assigned the mid-elevation (4,403 m) across the TP a value of one, with values linearly transitioning to zero at the maximum and minimum altitudes. We further quantified two other topographic variables: local range in elevation and surface area ratio of the physical terrain. We used the software ArcGIS v. 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA) to calculate: (a) elevation range, defined as the difference between the maximum and minimum altitude in each 0.5-degree × 0.5-degree grid cell; and (b) surface area ratio, measured using the DEM Surface Tools (Jenness, 2013). All topographic variables were derived from digital elevation maps (DEMs) obtained from the Consortium for Spatial Information (<https://www.cgiar-csi.org/>) and had a spatial resolution of 100 m × 100 m.

The third hypothesis concerning uplift reflects the *Climatic gradient* across the TP, where increases in bioclimatic disparities could have led to species diversification (Table 1). Under this hypothesis, high levels of SR and endemism would be found in areas of high bioclimatic stratification (Endler, 1982). To produce a minimum number of orthogonal climatic variables for each grid cell, we did a principal components analysis (PCA) using 10 bioclimatic variables (bio1, bio2, bio3, bio4, bio6, bio10, bio12, bio14, bio15, bio17) selected from the 19 complete bioclimatic variables of Hijmans, Cameron, Parra, Jones, and Jarvis (2005) (see Supporting Information Table S4 for the descriptions of the 19 variables) after removing collinearity with pairwise correlation $r > 0.95$. The 10 bioclimatic variables were standardized to a range of (0, 1) for the PCA. We used the first three climate principal components (PCs; explained 78.3% of total variation) to calculate the climatic gradient. Using the SDMT_{TOOLBOX} v. 1.1c (Brown, 2014), we calculated the heterogeneity (*SD* of each cell with the eight neighbouring cells) of each PC, weighted each PC heterogeneity layer by the amount of variation explained, and summed them to produce the climatic gradient (Figure 2c).

The fourth hypothesis associated with uplift was *Geographical isolation* (Table 1), producing genetic divergence that triggered speciation and allowed evolutionary areas where adjacent populations could hybridize (Vandergast et al., 2008). Here, we regarded congruent patterns of genetic divergence among different species

as indicative of geographical isolation. To quantify this, we first searched the phylogeographical literatures for Tibetan plant species. Among these studies, species have been investigated using several types of DNA markers (chloroplast, mitochondrial, nuclear). To ensure congruence in DNA markers, we mainly selected maternally inherited markers [e.g., chloroplast DNA (cpDNA) for angiosperms, mitochondrial DNA (mtDNA) for gymnosperms]. Ultimately, 52 species in the TP were determined (see Supporting Information Table S5, a list of the data sources is found in the Appendix). For each of these species, we gathered the geographical coordinates of each sampling location along with haplotype composition. Referenced DNA sequences were gathered in GenBank and then made these jointly into haplotype sequences. Based on these cpDNA or mtDNA haplotype sequences, we calculated genetic divergence values (D_A) (Nei & Li, 1979) among populations using the ARLEQUIN v. 3.5 package (Excoffier, Laval, & Schneider, 2005) under the Tamura and Nei (1993) model of nucleotide evolution. We finally mapped the divergence values at the geographical mid-points between populations and created a continuous pattern of genetic divergence for each species using an inverse distance weighted interpolation algorithm. To highlight the spatial concordance across species, the genetic divergence landscapes for all taxa were averaged into a single multispecies genetic landscape (Figure 2d). We rescaled each individual landscape by dividing each cell value by the grid maximum for each species to ensure equal weighting in the multispecies landscape. We used the GENETIC LANDSCAPE GIS TOOLBOX (Vandergast, Perry, Lugo, & Hathaway, 2011) to map genetic divergence landscapes for each species and the single multispecies landscape in ArcGIS v. 10.1.

2.4.2 | Hypotheses related to Quaternary climate fluctuations

The *Climatic stability* or *Refugia* hypothesis (Dynesius & Jansson, 2000; Vandergast et al., 2008; Table 1) proposes Quaternary climate oscillations generated glacial–interglacial disturbance cycles that forced species to either retreat to refugia, or disperse to other areas. In this study, we used bioclimatic data and genetic diversity mapping to quantify predictors for the hypotheses of *climatic stability* and Quaternary *refugia*.

We used available bioclimatic data for four separate time periods (Last Interglacial, Last Glacial Maximum, Mid-Holocene and current conditions; available at <https://www.worldclim.org/>; also see Supporting Information Table S4; Hijmans et al., 2005) to construct the spatial layer of *climatic stability*. After excluding the bioclimatic variables of high collinearity (Pearson's $r > 0.95$), we retained the same 10 bioclimatic variables as used in the PCA of Figure 2c. We then calculated the *SD* of each variable layer throughout the four time periods, summed these and inverted the result to create a spatial layer representing the climatic stability (Figure 2e).

A congruent genetic diversity pattern is a direct indicator of evolutionary *refugia* (Vandergast et al., 2008; Table 1). Based on the haplotype sequences of 52 species used to calculate the predictor

representing the geographical isolation hypothesis (see Supporting Information Table S5), we used the ARLEQUIN v. 3.5 package (Excoffier et al., 2005) to calculate the average sequence divergence among individuals (x_i) as genetic diversity value. Then, genetic diversity values were mapped at each sample location and interpolated in the same manner as the genetic divergence landscapes above. We used the GENETIC LANDSCAPE GIS TOOLBOX (Vandergast et al., 2011) to build a genetic diversity pattern for each species and summed these to create a single multispecies landscape for overall genetic diversity (Figure 2f).

For species adapted to montane areas, interglacial warmer temperatures can cause alpine taxa to migrate to higher elevations, potentially resulting in species divergence (Colinvaux, 1993; Table 1). This speciation model could result from both topographic heterogeneity and temperature instability. Following a similar approach as used to construct the climatic stability, we calculated the mean SD of low-correlated ($r < 0.95$) bioclimatic temperature layers (bio1, bio2, bio3, bio4, bio6, bio10) over the four time periods, and then summed these, multiplied by a standardized topographic heterogeneity layer to generate a predictor (Figure 2g). This variable was used to test the *Disturbance-vicariance* hypothesis.

Our final climate oscillations-related hypothesis is the *Dispersal corridor* hypothesis (Table 1). In phylogeographical studies, haplotype patterns among populations can reveal the population demographic history, especially rapid historical dispersal, such as occurred during the Quaternary (Chan et al., 2011). In population genetics, a shared haplotype between two populations indicates gene flow, hence a higher proportion of shared haplotypes could represent higher strengths of dispersal among localities. Another possibility is that species distribution within suitable habitat could have facilitated dispersal among populations. Therefore, by combining the shared haplotypes network and species distribution, we were able to estimate the historical *dispersal corridor* using the least cost path (LCP) method, a technique commonly used in landscape ecology. We obtained shared haplotypes patterns from the phylogeographical studies of 52 species in the TP (see Supporting Information Table S5) and estimated their distributions using the maximum entropy algorithm in MAXENT v. 3.3 (Phillips, Anderson, & Schapire, 2006). We then predicted the dispersal corridor for each species using the LCP approach implemented in the SDMTOLBOX v. 1.1c (Brown, 2014). We combined the individual dispersal layers to create a single concordant dispersal layer (Figure 2h).

2.5 | Statistical analysis

We rescaled all predictors to a resolution of 0.5-degree \times 0.5-degree and standardized them to a range of (0, 1) using min-max transformation. To explore any bivariate relationship between diversity and individual predictor at the scale of the entire TP, we calculated Pearson's correlation among response and predictor variables applying Dutilleul, Clifford, Richardson, and Hemon's (1993) method in the software SPATIAL ANALYSIS IN MACROECOLOGY (SAM; Rangel, Diniz-Filho, & Bini, 2010) to account for spatial autocorrelation.

To quantify the independent and combined contributions of the processes of Neogene plateau uplift and Quaternary climate fluctuations to species diversity, we used partial regression analysis to partition the effects of plateau uplift versus climate fluctuations on the total variance in diversity. All eight predictive variables as described above attributed to uplift and Quaternary climate changes were included, and hence we obtained an independent explanation of each process (uplift or climate changes) and their joint effect. This analysis was conducted using the R package Vegan (Oksanen et al., 2016).

To determine the independent influence of each hypothesized predictor in explaining the observed diversity patterns of endemic species of the TP, we also applied the method called orthogonally transformed beta coefficients (Brown, Cameron, Yoder, & Vences, 2014). This approach eliminates the influence of collinearity between variables (see Supporting Information Table S6), before determining the relative contribution of each predictor to species diversity while simultaneously considering the different causal processes. We first conducted a PCA for the eight predictive variables to obtain their component loadings (α_{ij}). Principal components for each grid cell were extracted and loaded as explanatory variables in the conditional autoregressive (CAR) model in SAM (Rangel et al., 2010). We then ran the multivariate CAR analysis iteratively until only those explanatory variables contributing significantly to the model at the 5% level were retained. Finally, the resulting standard beta coefficients (β_j) were multiplied by the relevant component loadings (α_{ij}), summed for each variable and converted to percentages to quantify the relative contribution for each predictor.

3 | RESULTS

3.1 | The diversity of Tibetan endemic seed plants

The TP is home to 3,673 endemic seed plant species that belong to 512 genera and 112 families (see Supporting Information Appendix S3). Most of these are herbaceous (2,775 species), with 742 being shrubs and 156 trees. There are clear spatial trends in the distribution of endemic plant diversity. SR and PD decrease from the southeast to the northwest of the TP and this pattern is consistent for all life-forms (Figure 3). Generally, species diversity is higher in the east and southeast of the plateau where the Hengduan and East Himalaya Mountains (HHM) are located. Shangri-La County in Yunnan Province has the greatest number of endemic species (918), while the lowest richness (average SR < 10) is found in the Qiangtang Plateau and West Kunlun Mountains to the northwest. SR and PD within life-forms are highly positively correlated ($r > 0.963$, $p < 0.01$; Supporting Information Table S7), but are relatively low between life-forms, particularly between herbaceous plants and trees ($r = 0.658\text{--}0.760$, $p < 0.01$). Woody plants (i.e., shrubs and trees) are concentrated in the mountains at the edge of the plateau with relatively low altitudes, while tree species are absent from the central and western regions with an elevation above 4,000 m. Across the TP, most predictor variables had a strong bivariate correlation with species diversity, but the strength of association differed between

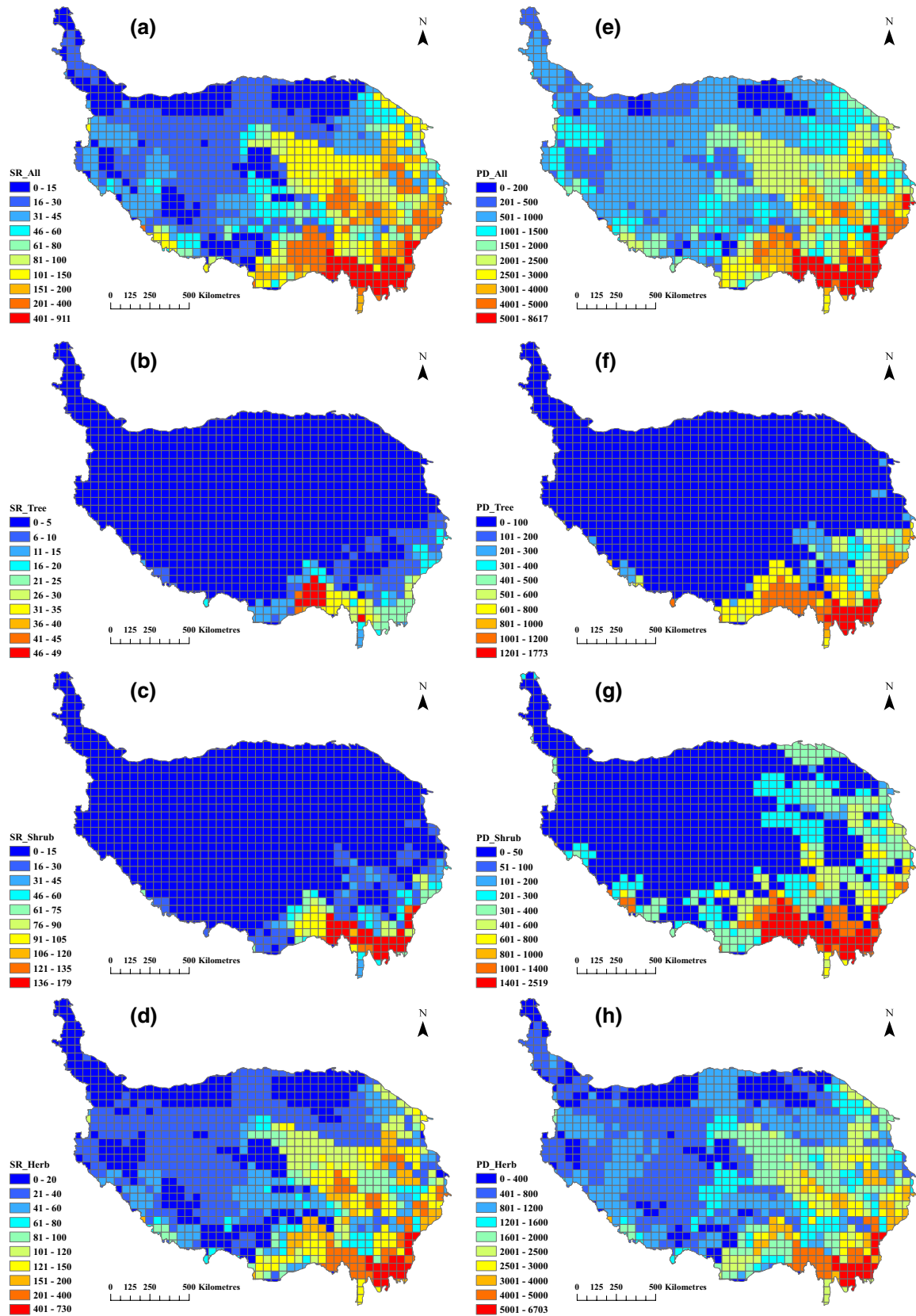


FIGURE 3 Spatial distributions of species richness (SR) and phylogenetic diversity (PD) for all the species (a and e), trees (b and f), shrubs (c and g) and herbaceous plants (d and h) in the Tibetan Plateau

life-forms, with topographic heterogeneity, climatic gradient and dispersal corridor all having significant correlations (range ~0.42–0.66; see Supporting Information Table S8).

3.2 | The contribution of plateau uplift and Quaternary climate fluctuations to plant diversity

Hypotheses associated with plateau uplift garner more support than those related to climate fluctuation, as plateau uplift independently accounted for more variance than climate fluctuations (13.8%–26.4% vs. 7.8%–15.0%; Table 2). There are also strong interactions between the two factors in the partial regression analysis (12.7%–29.0%; Table 2). Overall, half (mean = 52.4%) of the variance in total species

TABLE 2 Partial regression for partitioning the effects of plateau uplift and climate fluctuations on diversity patterns for different groups

	a	a:b	b	a + b	Residual
SR_All	0.213	0.152	0.111	0.477	0.523
SR_Tree	0.138	0.277	0.100	0.516	0.484
SR_Shrub	0.245	0.188	0.114	0.548	0.452
SR_Herb	0.193	0.127	0.106	0.426	0.574
PD_All	0.201	0.241	0.095	0.537	0.463
PD_Tree	0.264	0.261	0.150	0.675	0.325
PD_Shrub	0.161	0.290	0.078	0.530	0.470
PD_Herb	0.184	0.209	0.093	0.485	0.515

Note: a = explained variance by plateau uplift only; b = explained variance by Quaternary climate fluctuations only; a:b = shared explained variance; a + b = totally explained variance by both plateau uplift and Quaternary climate fluctuations; SR = species richness; PD = phylogenetic diversity.

diversity is explained by the combined effects of plateau uplift and climate fluctuations. However, explained variance differs between life-forms, being highest for trees (mean = 59.5%) and lowest for herbs (45.5%). Plateau uplift explains slightly more variance for shrubs (mean = 20.3%) than for trees (20.1%) and herbs (18.8%). By contrast, climate fluctuations explain more variance for trees (mean = 12.5%) than for herbs (9.9%) and shrubs (9.6%).

The mixed CAR models controlling for autocorrelation in the response variable suggest each variable (hypothesis) has a distinct but nondominant contribution to the diversity patterns (Figure 4; also see Supporting Information Table S9). The amount of variance explained by each variable differs little across SR, PD and life-form. In order of decreasing effect size, predictors explaining at least 10% of the variation in the response variables are montane museum (mean = 25.0%), geographical isolation (16.7%), climatic stability (13.5%) and refugia (13.2%). We found neither plateau uplift nor climate fluctuations dictated the formation of the diversity of the TP, although the former explained slightly more variance in endemic seed plants diversity than the latter. CAR models including all variables explained 37%–75% of the variance in species diversity, with the SR of shrub plants being best explained (75%).

4 | DISCUSSION

4.1 | The contribution of Neogene plateau uplift to species diversity

In line with studies of dated phylogeny (see Supporting Information Table S1 for references), we found evidence consistent with the hypothesis that plateau uplift generated species diversity in the TP through its influence on environmental conditions, such as

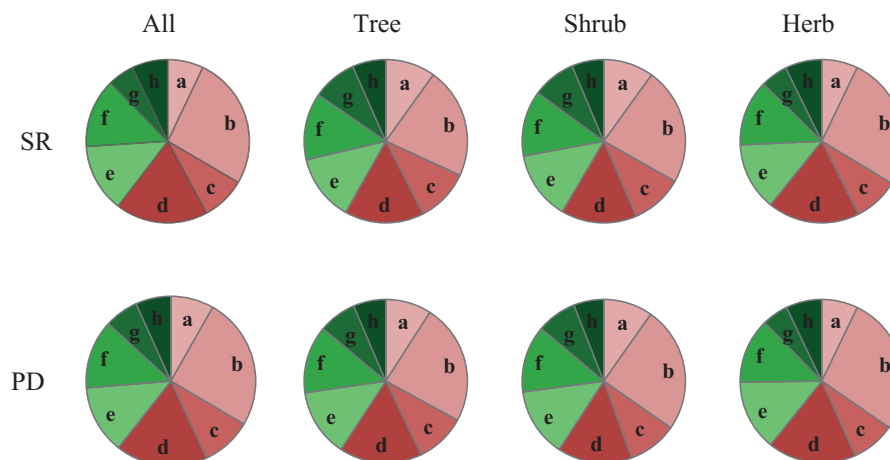


FIGURE 4 The relative contribution of each predictor to the observed diversity patterns in mixed conditional autoregressive (CAR) spatial models. SR = species richness; PD = phylogenetic diversity. The characters in the pie charts correspond to the predictors. Predictors related to the Neogene plateau uplift are (red colour): (a) topographic heterogeneity, (b) montane museum, (c) climatic gradient, (d) geographical isolation. Predictors related to the Quaternary climate fluctuations are (green colour): (e) climatic stability, (f) glacial refugia, (g) vicariance–disturbance, (h) dispersal corridor

topography and climatic conditions. This has been previously suggested (Mao et al., 2013; Yan, Yang, & Tang, 2013), but has not been explicitly tested until now. The climatic pattern and topographic features in the TP probably resulted from intense orogenic activities during the Neogene period (Li, Shi, & Li, 1995; Shi, Li, & Li, 1998). Thus, extensive plateau uplift was possibly the original trigger influencing this region's species diversity. The historical perspective linking past environmental changes with species diversification history in this way provides a powerful framework to extend the time-scale over which we can explore the biogeographical processes that shape current diversity patterns (Brown et al., 2014; Condamine, Rolland, & Morlon, 2013).

The four hypotheses that were based on Neogene plateau uplift gained more support in explaining species diversity than those related to Quaternary climate changes (Table 2). These hypotheses are related to a rapid diversification of lineages triggered by plateau uplift (Lu et al., 2018; Xing & Ree, 2017). From the evidence of the relative contribution of each predictor to species diversity (see Supporting Information Table S9), it seems likely that the four uplift-related predictors acted in a sequential fashion over time. The predictor representing the topographic heterogeneity hypothesis explained a small amount of variation in species diversity (explained 8.54% of variation on average), which presumably had an effect at the beginning of the Neogene period. Evidence suggests that the rapid plateau uplift during this period would have offered extensive new areas of high-elevation habitat, allowing species in the surrounding lowlands to become successively adapted to high altitudes through diversification (Favre et al., 2015). In these circumstances, areas with higher topographic heterogeneity could offer more vacant niches with specific climatic and microhabitat conditions, possibly explaining the high diversity in the southeast TP such as the HHM. Hence, these newly formed mountainous areas provided the template for species radiations during the early stage of plateau uplift, as has been found in other montane areas, such as the Andes (Luebert & Weigend, 2014) and Indian Ghats (Vijayakumar, Menezes, Jayarajan, & Shanker, 2016). With continuing uplift of the TP, the alpine zones such as the Hengduan Mountains would become many isolated "sky islands". It has been shown that long-term geographical isolation in the Hengduan Mountains and other mountainous areas further promotes allopatric speciation and increases endemism (Steinbauer et al., 2016; Xing & Ree, 2017). In this study, we confirmed topography-driven isolation was an important driver of species diversity (16.65%).

During the Late Miocene, possibly due to the TP uplift, the Indian and East Asian monsoon progressively intensified, generating a climatic gradient with warm and humid conditions in the southeast grading to a cold and dry northwest (An, Kutzbach, Prell, & Porter, 2001). The hypothesis of parapatric speciation along climatic gradients (Endler, 1982) predicts SR and endemism to be highest in areas of high bioclimatic stratification. We found evidence consistent with this hypothesis that areas of high bioclimatic stratification (e.g., the HHM region) were rich in species (Figure 2c). Meanwhile, the predictor representing the climatic

gradient hypothesis explained 8.72% and 9.58% of variation in total SR and PD, respectively (see Supporting Information Table S9). Compared to the allopatric speciation (e.g., resulting from geographical isolation) regularly tested in the TP (Wen et al., 2014; Xing & Ree, 2017), we found parapatric speciation implied by this hypothesis played a moderate role in shaping the diversity patterns. Beyond the TP, this hypothesis obtained a similar level of support (10.5%) in a study explaining the diversity of the amphibians and reptiles of Madagascar (Brown et al., 2014).

During the early Neogene, the plateau likely reached 3,000–4,000 m in elevation (Shi et al., 1998), and multiple plant diversifications appear to have occurred around this period (see Supporting Information Figure S1). This altitude range is the present intermediate zone of the TP and harbours the most endemic species (see Supporting Information Figure S3). The additional time for speciation and the accumulation and persistence of lineages after the early Neogene (c. 20 Ma) would explain the currently observed patterns. This is consistent with the montane museum hypothesis, which explained the greatest amount of variation in our analysis and has prior support in the TP (Favre et al., 2016; Li et al., 2009) and other montane regions (e.g., Hutter, Guayasamin, & Wiens, 2013).

4.2 | The contribution of Quaternary climate fluctuations to species diversity

The last glaciation strongly affected species distribution in Europe and North America owing to the formation of a large ice sheet (Soltis, Morris, Mclachlan, Manos, & Soltis, 2006; Taberlet, Fumagalli, Wust-Saucy, & Cosson, 1998). No equivalent large ice sheet formed across the TP during the Quaternary (Li & Li, 1991), but we found cyclic glacial-interglacial periods influenced diversity patterns, based on the role of glacial refugia (see Supporting Information Table S9). In this study, there were two types of refugia. The first is predicted from relative climatic stability throughout the glacial-interglacial cycles, the other is identified based on phylogeography. These refuge types partially converged within the HHM region, suggesting conditions in this region facilitated survival of many plants and some animal species during the glacials (Liu et al., 2016; Zhan, Zheng, Wei, Bruford, & Jia, 2011). We also found some local high diversity areas in the "platform" region of the TP, such as the Three Rivers Headstream and the Yarlung Zangbo Valley (Figure 2f), areas that supported micro-refugia during the glaciation (Liu, Duan, Hao, Ge, & Sun, 2014). Refugia are often found to be important in promoting and maintaining diversity in diverse biomes and biotic groups, for example, mite diversity in the wet tropics of Australia (Boyer, Markle, Baker, Luxbacher, & Kozak, 2016).

We found vicariance resulting from fluctuations in temperature that created isolated populations (disturbance–vicariance) had a limited effect on diversity patterns of the TP (6.89%). This could be related to the distribution of several alpine plants favoured in colder environments contracting to isolated mountain-top areas during the interglacials (Liang et al., 2018). The resulting long-term vicariance among taxa would accelerate population divergence and endemism (Steinbauer et al., 2016).

Evidence has shown that few species in the TP were able to disperse widely and expand their populations during the Quaternary (see Supporting Information Figure S2). This likely explains the limited support for the dispersal corridor hypothesis, which explained little of the variation in the two diversity measures (see Supporting Information Table S9). Despite the limited effect here, the identification of areas where dispersal is favoured is nonetheless important for contemporary biodiversity conservation (Trakhtenbrot, Nathan, Perry, & Richardson, 2005). Most dispersal corridors we identified were located within the HHM region, suggesting that mountainous areas acting as dispersal corridors promoted effective movement of species (Luebert & Weigend, 2014). This represents an important conservation priority complementary to those associated with extant diversity emphasizing the importance of protecting this region.

4.3 | No dominant, single hypothesis for patterns of diversity

In this study, we found that no single hypothesis garnered overwhelming support as an explanation for the patterns of species diversity of the TP. Rather they reflect complex interacting historical processes, which is perhaps not surprising given the long-term accumulation of the diversity in the region. This result is also consistent with other studies such as that explaining the biogeography of the amphibians and reptiles in Madagascar (Brown et al., 2014) as well as those explaining the rapid diversification in Andean bellflowers (Lagomarsino et al., 2016) and insects (Legendre & Condamine, 2018).

Generally, differences in SR may be explained by two main hypotheses: the diversification rate hypothesis (Ricklefs, 2007) and the clade age (time) hypothesis (Stephens & Wiens, 2003). This represents an alternative means to group the hypotheses we investigated in this study, where the diversification rate hypothesis would occur under topographic heterogeneity, climatic gradient, geographical isolation and disturbance–vicariance, while the clade age hypothesis would correspond to mechanisms proposed under the montane museum, climatic stability, refugia hypotheses. Based on the history of TP uplift and the diversification time of several clades (see Supporting Information Table S1), the speciation time of most plant species in the TP is not long in the evolutionary time-scale. As evidence has suggested that clade age is more important for explaining richness patterns over shorter time-scales (Pontarp & Wiens, 2017; Wiens, 2017), accordingly we found the time hypothesis garnered slightly more support in explaining the diversity patterns (52%) than the diversification rate hypothesis (48%). However, the latter still gains strong support as an explanation for the formation of species diversity (Alfaro et al., 2009; Rolland, Condamine, Jiguet, & Morlon, 2014). A recent study suggests that the rate of in situ diversification increased when the Hengduan Mountains (HM) uplifted about 8 Ma (Xing & Ree, 2017). This region is not only a major hotspot of species diversity, but also possesses high environmental heterogeneity and

numerous geographical barriers. Thus, we assume the complex ecological and geographical conditions in the HM accelerated the diversification rate, further promoting the establishment of the high biodiversity. As is the case for the large-scale environmental processes of uplift and climate fluctuations, the two speciation hypotheses (time and diversification rate hypothesis) are non-exclusive and together garner strong support as explanations for the species diversity in the TP.

4.4 | Diversity patterns and implications for conservation

Understanding spatial patterns of diversity is important in conservation planning for endangered species, or those with highly localized distributions (Kremen et al., 2008). Most endemic seed plants of the TP are alpine plants, cold-adapted species that survive only in a high-elevation environment. As a result, they are highly susceptible to climate warming and represent a conservation priority (Cannone, Sgorbati, & Guglielmin, 2007). The highest endemic seed-plant diversity in the TP is in the HHM, a region that is already regarded as a hotspot at national and global scales for a broad range of organisms (Huang et al., 2016; López-Pujol, Zhang, Sun, Ying, & Ge, 2011; Myers et al., 2000). Our study supports calls for protection of this whole area. We also call for conservation attention to areas of the central and northwestern TP where there are very few endemic plants, but the low-diversity system is particularly vulnerable to increasing degradation of grasslands, and desertification and climate change (Harris, 2010).

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DATA ACCESSIBILITY

The species list, distributions, and dated phylogeny of Tibetan endemic seed plants for this study are provided in the Supporting Information.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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