Concealed truth: Modeling reveals unique Quaternary distribution dynamics and refugia of four related endemic keystone Abies taxa on the Tibetan Plateau

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Abstract

Understanding the factors driving the Quaternary distribution of Abies in the Tibetan Plateau (TP) is crucial for biodiversity conservation and for predicting future anthropogenic impacts on ecosystems. Here, we collected Quaternary paleo-, palynological, and phylogeographical records from across the TP and applied ecological niche models (ENMs) to obtain a profound understanding of the different adaptation strategies and distributional changes in Abies trees in this unique area. We identified environmental variables affecting the different historical biogeographies of four related endemic Abies taxa and rebuilt their distribution patterns over different time periods, starting from the late Pleistocene. In addition, modeling and phylogeographic results were used to predict suitable refugia for Abies forrestii, A. forrestii var. georgei, A. fargesii var. faxoniana, and A. recurvata. We supplemented the ENMs by investigating pollen records and diversity patterns of cpDNA for them. The overall reconstructed distributions of these Abies taxa were dramatically different when the late Pleistocene was compared with the present. All Abies taxa gradually receded from the south toward the north in the last glacial maximum (LGM). The outcomes showed two well-differentiated distributions: A. fargesii var. faxoniana and A. recurvata occurred throughout the Longmen refuge, a temporary refuge for the LGM, while the other two Abies taxa were distributed throughout the Heqing refuge. Both the seasonality of precipitation and the mean temperature of the driest quarter played decisive roles in driving the distribution of A. fargesii var. faxoniana and A. recurvata.
These four related taxa of *Abies* in the TP face serious threats due to habitat destruction and climate change (Xiang & Rushforth, 2013a, 2013b). Rising temperature and extreme precipitation have been highlighted as major factors driving the population dynamics of *Abies* taxa (He et al., 2015; Wang, Xu, et al., 2017). Further, as explained by Ordonez and Svenning (2016), historic climate data have proved instrumental for describing past events and explaining the current distribution of species. Paleoecology can provide further insight for understanding the long-term influence of environmental changes on *Abies* taxa and their ecosystems (Tinner & Valsecchi, 2013). Also, accurate responses of plant distributions to historical climate change could serve as good predictors of ongoing climate change (Waltari et al., 2007; Willis & McElwain, 2002). Both Asian Monsoon and uplifting of the TP during the Eocene which created a unique climatic conditions have influenced the distribution and diversification of *Abies* in this area (Cao, Herzschuh, Ni, Zhao, & Böhmer, 2015; Xiang, Cao, & Zhou, 2007). Yet, studies of the driving factors or dynamics of spatial distribution patterns of *Abies* taxa and their response to habitat changes at the TP remain surprisingly limited (Xiang et al., 2006). Knowing which factors drove historical changes in *Abies* distributions might help enhance mitigation strategies for its species and contribute to the conservation of the Tibetan forests in the face of projected climate change scenarios. Ecological niche models (ENMs) can offer perspectives for answering inquiries concerning species’ historic and future potential distributions (García-Callejas & Araújo, 2016; Shrestha & Bawa, 2014). Not surprisingly then, ENMs are widely used for species distribution modeling (Dan & Seifert, 2011; Elith & Leathwick, 2009) and for assessing the degree of ecological segregation among different co-occurring taxa (Yi, Cheng, Wieprecht, & Tang, 2014). By applying ENMs to paleo-climate data, we can elucidate the potential past distributions of species (Du, Hou, Wang, Mao, & Hampe, 2017).

Based on pollen fossil records supported by other biological evidence, the climatic oscillations during the Quaternary period significantly influenced biome shifts at the TP (Zhang, Fengquan, & Jianmin, 2000). Evidence from its fossil records revealed the TP served as a vital refugium for numerous plant species that survived the Quaternary glaciations, including those of *Abies* (Wang & Liu, 1994). The southeast region of the TP provided refugia for the northerly biome during the Quaternary glaciation while it gradually retreated from north to south (Du et al., 2017). Identification of Quaternary refugia is based on various forms of historical biogeographic evidence, particularly those derived from paleo-ecological...
studies. Such evidentiary studies helped to identify glacial refugia in the TP over the most critical periods of the Pleistocene for exemplary taxa including *Ginkgo biloba, Pedicularis longiflora, Primula secundiflora*, evergreen oaks (*Quercus aquifolioides*), and *Primula sikimensis* (Du et al., 2017; Gong, Chen, Dobes, Fu, & Koch, 2008; Wang, Gong, Hu, & Hao, 2008; Yang, Li, Ding, & Wang, 2008). Knowledge of Quaternary refuge distributions of species long ago (Cao et al., 2015), as well as remaining refuge distributions under current climate change conditions (Tinner & Valsecchi, 2013), can inform the future protection of *Abies* trees against climate change. Several studies have addressed the biogeographic history of *Abies* species in the TP (e.g., Peng et al., 2015; Shao, Zhang, Phan, & Xiang, 2017; Xiang et al., 2015), but a thorough understanding of it still eludes us. This may be due, in part, to the lack of using integrative approaches that incorporate both palynological and phylogeographical data. The inherent biases and complexities of the palynological approach—its limitation for providing *Abies* taxonomic identifications to the species level, dearth of taxonomic precision, inability to account for underrepresented taxa in fossil records, and underestimation of migration distances and shifts in some *Abies* species distribution—have collectively hindered its ability to infer the location and timing of refugia. This has added to the difficulty in defining the spatial and temporal range of distribution of various species in the past.

This study applied ENMs to integrated paleo-climatic data, fossil pollen records, and previous phylogeographic data of *Abies* taxa for modeling and describing the current and Quaternary distributions of four endemic *Abies* taxa. Through the use of this integrative approach, we sought to provide a better understanding of how climate fluctuations have impacted the distribution dynamics of *Abies* taxa in Hengduan Mountains biodiversity hotspot.

Ecological niche models, *Abies* paleo-records, and phylogeography each presumes certain stability to some extent in ecological niche dimensions. Nonetheless, the integration of these employed approaches may offer better insight while also improving the accuracy of ENM applications intended to predict the potential Quaternary refugia of the study area. We hypothesized that the different adaptation strategies driven by environmental factors resulted in differing distribution patterns for the four endemic *Abies* in this area in the late Pleistocene. A better understanding of divergent adaptation strategies of *Abies* species may thus provide an effective instrument to robustly identify those vulnerable areas for which proactive conservation measures are needed in the high-altitude region of the TP.

2 | METHODS

2.1 | Study area and species

The TP is surrounded by the Himalayan Mountains to the south, the Kunlun and the Qilian Mountains to the north, the Pakistan Karakorum Mountain range stretches along its west side, while the mountains of Hengduan border the east side of the plateau (Zhang, Li, & Zheng, 2002; Figure 1). Subalpine coniferous forest composed of *Abies* and *Picea* is the dominant forest type mainly covering the southeastern region of the TP (Li, 1993; Mackinnon et al., 1996). *Abies fargesii var. faxoniana* is the representative tree taxon of dark coniferous forests distributed in the northern part of the Hengduan Mountains area, east of the TP (Guan & Zhou, 1983), bordered to the east by the Longmen Mountains, to the west by Jinchuan County, and to the north by the Balang Mountains and Tao River Basin, with an elevation range of 2,500–3,000 m a.s.l. (Xiang et al., 2006). *Abies recurvata* is an endemic species in the TP; it grows along the basin of Bailongjiang River south of Gansu Province and in the north and northwest of Sichuan Province, across a broad elevation of 2,300–3,600 m a.s.l. Both *A. forrestii* and *A. forrestii var. georgei* are the main taxa of the forest south of Hengduan Mountains, at the southeastern side of the TP (China Forest Editorial Board, 1997; Fang et al., 2011). *Abies forrestii* grows mainly in southwest

![FIGURE 1 Current distribution localities of the four endemic Abies across the Tibetan Plateau](image-url)
Sichuan Province and the northern part of Yunnan Province, eastern Tibetan, as well as in Kachin State in Myanmar and Bhutan (Fang et al., 2011). Abies forrestii var. georgei is distributed mainly in southwestern Sichuan and northwestern Yunnan and occurs from the eastern section of the Brahmaputra River in Tibet to downstream of the Yalong River located in Sichuan Province (China Forest Editorial Board, 1997). Abies forrestii var. georgei is found at 3,500–4,500 m a.s.l., while A. fargesii var. faxoniana grows at a lower elevation, from 2,500 to 3,000 m a.s.l. (China Forest Editorial Board, 1997). Recently, A. recurvata and A. fargesii var. faxoniana have been accorded conservation status, being judged vulnerable taxa (Xiang & Rushforth, 2013a, 2013b), while the status of A. forrestii var. georgei is currently of least concern (Zhang, Katsuki, & Rushforth, 2013b) and that of A. forrestii (syn. A. forrestii var. forrestii) is considered as near-threatened (Zhang, Katsuki, & Rushforth, 2013a). Studies have suggested the taxonomic boundaries are well-established at the species and intraspecific levels of the Abies genus (e.g., Aguirre-Planter et al., 2012; Cinget, Lafontaine, Gérardi, & Bousquet, 2015; Shao & Xiang, 2015; Shao et al., 2017; Wang, Abbott, Ingvarsson, & Liu, 2014); however, their intrageneric classification is an active area of research (Eckenwalder, 2009; Farjon, 2010). These four taxa selected for study vary in their morphological traits and have dissimilar environmental requirements, according to information from other studies (e.g., China Forest Editorial Board, 1997; Guan & Zhou, 1983; Shao et al., 2017).

2.2 | Taxa occurrence data

Occurrence records of the four Abies taxa were obtained from a field survey conducted in September 2015 and June 2016, and from collected data archived in numerous databases, namely: the GBIF (Global Biodiversity Information Facility, http://www.gbif.org), the CVH (Chinese Virtual Herbarium, http://www.cvh.org.cn/), the NSII (National Specimen Information Infrastructure, http://www.nssi.org.cn/), and other related sources (see all references in the “Additional Reference List” in Appendix S1). Redundant points were removed to ensure a minimum of 1,000 m was maintained as the distance separating data records, to minimize the influence of spatial autocorrelation on the modeling results. In total, 212, 69, 184, and 220 valid effective occurrence records for these four taxa were collected (Figure 1).

2.3 | Environmental data and selection of variables

To represent the environmental conditions in different climatic periods, 19 bioclimatic predictors obtained from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) were used, in addition to two indirect gradients predictors (slope and aspect). Downscaled data from two general circulation models (GCMs), namely the CCSM4 and MIROC-ESM (Brady, Otto-Bliesner, Kay, & Rosenbloom, 2013; Raes et al., 2014; Sueyoshi et al., 2013), were used to obtain climatic data for the LGM (21 kyr BP) and the mid-Holocene (6 kyr BP). The LIG data (120–140 kyr BP), with a spatial resolution of 30 arc seconds, were obtained following Otto-Bliesner, Marshall, Overpeck, Miller, and Hu (2006) from the WorldClim 1.4 (http://www.worldclim.org; Hijmans et al., 2005). The last two variables corresponded to indirect abiotic gradients: The slope and aspect derived from the digital terrain model (DTM) were extracted from the Shuttle Radar Topography Mission (SRTM) (http://srtm.csi.cgiar.org/) at 30 arc-second resolution. Principal component analysis (PCA) was performed on standardized and centered data of the 19 current bioclimatic predictors and two indirect gradients (Raes et al., 2014). The first three components (PCs) accounted for 98.48% of the variance in the dataset employed in the analysis (Figure S1).

Multicollinearity can cause the mode to overfit the data used. Therefore, the Pearson correlations were tested for all pairwise combinations of the 19 climate datasets (Raes et al., 2014). The SDMtoolbox (Brown, 2014; Brown, Bennett, & French, 2017) was used within the framework of ArcGIS 10.0 (ESRI, Redlands, CA, USA) to conduct a correlation analysis among the 19 climate datasets’ variables’ grids that represented the study area. Only uncorrelated variables with a spatial correlation value below 0.75 were retained (Table S1; Raes et al., 2014). To calibrate the ENMs for each species, nine selected predictive variables were used: mean diurnal range (MDR), temperature annual range (TAR), mean temperatures of driest (TDQ) and wettest (TWQ) quarter, precipitation of wettest (Pmax), driest month (Pmin), precipitation of seasonality (PS), and warmest (PHQ) and coldest (PCQ) quarter, along with another two predictors: slope and aspect.

2.4 | Modeling algorithm: Maxent

The maximum entropy (Maxent) modeling technique (Phillips, Anderson, & Schapire, 2006) was applied to the above data, it being one of the most commonly used and accurate ways to predict species’ distributions and habitat suitability (Dan & Seifert, 2011; Elith & Leathwick, 2009). The models for each taxon were first calibrated for the current distributions relative to the current climate; the most accurate models were then applied to the historical data (LIG, LGM, mid-Holocene) to get predictions for those past periods. The occurrence records datasets were randomly split (75%–25%), where the 75% portion for each taxon was used to calibrate the algorithm, and the remaining 25% used for evaluating the produced ENMs (Bueno et al., 2017). The version of Maxent used was obtained from http://biodiversityinformatics.amnh.org/open_source/maxent/; for each taxon, n = 200 replicate runs were undertaken in Maxent 3.4.0.

2.5 | Model calibration and evaluation

The ENM models developed to determine the potential distribution of Abies taxa had a logistic output format, which quantifies habitat suitability as a continuous probability value ranging from 0 to
1 (Phillips & Dudik, 2008). The potential distribution curves were estimated for each predictor, and the percentage corresponding to the relative contribution of each one to the habitat suitability models were assessed using Maxent's built-in jackknife test. To evaluate the models and assess their performance, the receiver operating characteristic (ROC) curve was plotted, for which the area under the curve (AUC) was estimated at the possible thresholds (Raes et al., 2014). The ROC curve is generated by plotting the sensitivity versus 1−specificity for the entire set of runs. The AUC provides a widely used metric of model accuracy (Fielding & Bell, 1997). Models attaining an AUC value > 0.7 are deemed of acceptable performance (Swets, 1988).

The response curves for the predictors used in building the models were then generated. Through them, we could gain insight into the quantitative relationships among investigated environmental predictors and the logistic probability of species existence. More specifically, such response curves mirror the favorable ecological niche of the species (Dan & Seifert, 2011).

To minimize the biases to the objective methods that integrated sensitivity with specificity, the maximum training sensitivity plus specificity (Tmax) and the minimum training presence (Tmin) logistic thresholds (Vedelsrønse, Tovarano, Becher, Balslev, & Barfod, 2013) were each retrieved from Maxent. This was done in addition to using the normal rank grading method (Raes et al., 2014).

2.6 | Multivariate analysis of bioenvironmental data

Redundancy analysis (RDA) was conducted for a relative assessment of the different environmental requirements of Abies forrestii, A. fargesii var. faxoniana, A. fargesii var. georgei, and A. recurvata. The RDA was performed on the set of environmental variables, based on their relative contribution percentage to the species habitat suitability models produced by Maxent (mean diurnal range, temperature annual range, mean temperature of wettest/driest quarter, precipitation of seasonality, precipitation of warmest/coldest quarter, and slope), ranked according to their quantitative importance by a forward selection process. Those variables were used to analyze the effect of climate and topography on the pattern of four Abies taxa distributions. The R software environment and its "vegan" package (R Development Team, 2008) were used to carry out this statistical analysis and produce its graphics.

2.7 | Paleoclimate, fossil, and phylogeographic records

Climate variables representing the LGM and the mid-Holocene paleoclimates were obtained from CCSM4 and MIROC-ESM general circulation models (GCMs) for inclusion in the analysis. Furthermore, data from the last interglacial period (Otto-Bliesner et al., 2006) were obtained from sporopollen, carbon isotope measurements, calcium carbonate, and ice cores for the area under study (Table A2). According to our review, the fossil and pollen sequences dated from or around the 6 kyr BP, 21 kyr BP, and 120–140 kyr BP periods in the TP (Table 1). Indications of when the assessed pollen sequence chronology overlapped with the LIG, LGM, or mid-Holocene periods are given in Table 1. Published cpDNA data were used to derive diversity patterns for use in the phylogeographical validation of the model hypotheses (Peng et al., 2012; Zhan, 2011). Since phylogeographical investigations of Abies taxa are limited at the TP, the evaluation of published cpDNA trnL-F, trnS-G, and ndhC data was possible for only two Abies taxa, namely A. fargesii var. faxoniana (Zhan, 2011) and A. recurvata (Peng et al., 2012) (Table S3; Appendix S1). Additional details on the genetic diversity index and expansion calculations are given as Appendix S1.

3 | RESULTS

3.1 | Climate scenarios

The summarized data for 14 deposits of the LGM and the mid-Holocene obtained from the final interpolated models (CCSM4 and MIROC-ESM), and for one point of the LIG climate data for TP, are presented in Tables S2 and S4. Also provided in Table S2 are the discrepancies between GCMs’ values through the CCSM4 and MIROC-ESM simulations and the paleoclimates, which were obtained from calcium carbonate, sporopollen, and ice cores for the different climate scenarios applied. Annual mean temperature (Tann) and annual precipitation (Pann) had consistently higher accuracy in the CCSM4 than MIROC-ESM simulation, but with no significant differences for the mid-Holocene in the CCSM4 and MIROC-ESM simulations. In general, the temperature simulations by the CCSM4 and MIROC-ESM models for the LGM were better than those for the mid-Holocene, while precipitation simulations were better than temperature simulations for all periods.

3.2 | Potential distributions of Abies taxa in the LIG, LGM, and mid-Holocene

The resulting ENMs provided high AUC scores (A. forrestii: 0.986 ± 0.002; A. fargesii var. faxoniana: 0.988 ± 0.002; A. fargesii var. georgei: 0.986 ± 0.002; and A. recurvata: 0.996 ± 0.002 (Figure S2). In comparing the projection for the LGM, based on both CCSM4 and MIROC-ESM GCM climate models, and that of LIG with the present day (Figures 3 and S3), evidently their general reconstructed distributions were significantly different, but not so for the mid-Holocene (Figures 2, 3, and S3). In particular, a contraction in the continuity of the four related species’ suitable area can be noticed across the southern part of the Hengduan Mountains—along with the Yangtze River, the Mekong River, and the Salween River—and in the eastern TP area. By contrast, an expansion in the northern and western TP between the LIG and the present can be observed (see Figures 2, 3, and S3; Table 2). Corresponding expansions of A. forrestii, A. fargesii
TABLE 1  Comparison between published pollen records and model predictions for forest occurrence at LIG (120–140 kyr BP), LGM (21 kyr BP), and mid-Holocene (6 kyr BP) as shown in the stability area map of Figures 3 and S3 (unless otherwise specified)

| Code | Site name | Latitude longitude | Estimated chronology (kyr BP) | Site type | Reference | Model prediction | Match between model by CCSM (MIROC) and data |
|------|-----------|----------------------|-------------------------------|-----------|-----------|------------------|-------------------------------------------|
| 1    | Heqing Basin, Yunnan Province | 25.850N 100.483E | 349–128 | Abies spp. | Xiao et al. (2006) | Inside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2    | Kunming Basin, Yunnan Province | 25.250N 102.517E | 201–120 | Tsuga chinensis, Chenopodiaceae, Quercus spp., Gramineae | Xu et al. (2009) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–1  | Diancang Mountain, Dai, Yunnan Province | 25.646N 100.109E | 122–118 | Abies spp. | Kuang et al. (2002) | Inside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–2  | Beihai Lake, Tengchong, Yunnan Province | 25.250N 102.517E | 150–126 | Abies spp. | Bao (2010) | Inside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–3  | Zhang'an, Pinglang, Gansu Province | 35.568N 105.007E | 200–140 | Corylus spp., Nitraria spp., Ephedra spp., Chenopodiaceae, Compositae, Pinus spp., Quercus spp., Chenopodiaceae, Gramineae | Liu and Su (1994) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–4  | Xiyan Mountain, Huining, Gansu Province | 35.658N 105.007E | 200–140 | Tamaricaceae, Pinus spp., Betula spp., Quercus spp., Corylus spp. | Liu (1992) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–5  | Luoquan, Gansu Province | 35.717N 109.517E | 127–123 | Betulaceae, Chenopodiaceae, Urticaceae, Chenopodiaceae, Compositae, Rosaceae, Urticaceae, Compositae, Humulus, Ranunculaceae, Cruciferae | Li (2008) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–6  | Naqu, Tibet | 31.467N 91.508E | 116–37 | Selaginella spp., Lycopodium spp., Osmunda spp., Pleuromanes spp., Cyathea, Asplenium spp., Filicinaceae, Concentricystes spp., Carya spp., Aquifoliaceae, Pinus spp., Quercus spp. | Zhao et al. (2005) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–7  | Qi Mountain, Shaanxi Province | 34.456N 107.623E | 128–10 | Quercus spp., Alnus spp., Carpinus spp., Ulmus spp., Corylus spp., Juglans spp., Pterocarya spp., Platycarya spp., Artemisia spp. | Zhao and Huang (1999) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–8  | Wugong, Shaanxi Province | 34.232N 109.367E | 110–100 | Artemisia spp., Pinus spp., Betula spp., Quercus spp., Alnus spp., Corylus spp., Convolvulaceae spp., Lycopodium spp., Juglandaceae spp., Morus spp., Acer spp., Pterocarya spp., Fagus spp., Selaginella spp., Polygonum spp. | Liu (1989) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 2–9  | Zari, Tibet | 30.928N 85.626E | 120–119 | Pinus spp., Chenopodiaceae, Gramineae, Cyperaceae | Yu (2008) | Outside area of stability at LIG | Yes, model by Otto-Bliesner et al. (2006) |
| 3    | Luoji Mountain, Xichang, Sichuan Province | 27.756N 102.328E | 22 | Abies spp. | Jiang et al. (2000) | Inside area of stability at LGM | Yes (Yes) |
| 4    | Heqing Basin, Yunnan Province | 25.850N 100.483E | 28.87–16.98 | Abies spp. | Xiao et al. (2006) | Inside area of stability at LGM | Yes (Yes) |

(Continues)
| Code | Site name | Latitude   | Longitude   | Estimated chronology (kyr BP) | Site type | Reference* | Model prediction | Match between model by CCSM (MIROC) and data |
|------|-----------|------------|-------------|-----------------------------|-----------|------------|------------------|------------------------------------------|
| 5    | Hongya County, Sichuan Province | 29.583N 102.433E | 22.5–20.5   | Abies spp.                 | Shi (2012) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 6    | Butuo County, Southwestern Sichuan Province | 27.717N 102.867E | 22.0–11.8   | Abies spp.                 | Liu et al., (2003) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 7    | Northwest of Daliang Mountain, Sichuan | 28.100N 103.500E | 30–14       | Abies spp.                 | Liu et al., (2003) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 8    | Yanbian County, Sichuan Province | 26.734N 101.653E | 25.6       | Abies spp.                 | Ye et al., (1986) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 9    | Lugu Town, Manning County, Sichuan Province | 28.283N 102.183E | 22         | Abies spp.                 | Cheng (2010) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 10   | Xiaohaizi, Leibo, Sichuan Province | 28.412N103.781E | 16         | Abies spp.                 | Liu et al., (2004) | Inside area of stability at LGM | Yes (Yes for Tmin area) |                                          |
| 11   | Wuben Village, Panzhihua City, Sichuan Province | 26.689N 101.725E | 20.455      | Abies spp.                 | Ye et al., (1986) | Inside area of stability at LGM | Yes (Yes)                     |                                          |
| 12   | Jiantang County, Shangri-la County, Yunnan Province | 27.817N 99.700E | 16.552–16.952 | Cornopteris acutiloba, Blechnum melanopus, Gymnotheca involucrata, Acorus calamus, Selaginella doederleini, Peperomia dulcoulxii, Girardiella palmata | Shi (2012) | Outside area of stability at LGM | Yes for Tmax area (No) |                                          |
| 13   | Jiantang County, Shangri-la County, Yunnan Province | 27.817N 99.700E | 24.827–25.458 | Gymnotheca involucrata, Acorus calamus, Isoetes japonica, Tamarix chinensis, Cedrus deodara, Fokienia hodginsii, Dichondra rotundata, Barbula rigida, Helwingia japonica | Shi (2012) | Outside area of stability at LGM | Yes for Tmax area (No) |                                          |
| 14   | Daganba, Guizhou Province | 26.500N 105.700E | 23         | Pinus spp., Fagus spp., Quercus spp., Cyperaceae, Gramineae | Han and Yu (1988) | Outside area of stability at LGM | Yes (Yes for Tmax area) |                                          |
| 15   | Shilong Village, Caohai, Bijie City, Guizhou Province | 26.800N 104.167E | 22         | Pinus spp., Salix spp., Cyperaceae, Gramineae, Lycopodium japonicum | Chen (1987) | Outside area of stability at LGM | No (No)                      |                                          |
| 16   | Kunming Basin, Yunnan Province | 25.250N 102.517E | 30–20      | Pinus spp., Artemisia spp., Chenopodium caespitosum, Myriophyllum verticillatum | Xu et al. (2009) | Outside area of stability at LGM | No (No)                      |                                          |
| 17   | Zhaojiayuanzhi, Caohai, Bijie City, Guizhou Province | 26.888N 104.221E | 21.0–19.1  | Cyclobalanopsis spp., Fagus spp., Quercus spp., Eucalyptus, Betulaeae, Pinus spp., Tsuga | Chen et al. (1993) | Outside area of stability at LGM | No (No)                      |                                          |
| 18   | Hongya County, Sichuan Province | 29.583N 103.267E | 22.5–20.5  | Deciduous broad-leaved forest (Hicriopteris glauca, Polypodium chinenensis, Alnus cremaschyna, Alnus ferdinandicolburgii, Acorus calamus, Saururus chinensis, Cyclobalanopsis glauca, Pinus spp., Tsuga dumosa, Morus alba) | Shi (2012) | Outside area of stability at LGM | Yes (Yes)                     |                                          |

*References: Shi (2012), Liu et al., (2003), Ye et al., (1986), Ye et al., (1988), Cheng (2010), Liu et al., (2004), Ye et al., (1986), Chen (1987), Han and Yu (1988), Xu et al. (2009), Chen et al. (1993), Shi (2012).
| Code | Site name                      | Latitude longitude | Estimated chronology (kyr BP) | Site type       | Reference          | Model prediction                                                                 |
|------|--------------------------------|--------------------|-------------------------------|-----------------|-------------------|-------------------------------------------------------------------------------|
| 2–10 | Peigucuo Lake, Tibet           | 28.001N 85.001E    | 31–15                         | Abies spp.      | Yu (2008)         | Inside area of stability at LGM Yes (Yes)                                     |
| 2–11 | Lantian, Shaanxi Province      | 34.154N 109.331E   | 85–10                         | Abies spp.      | Li (2005)        | Inside area of stability at LGM Yes for Tmin area (No)                        |
| 2–12 | Diexi, Sichuan Province        | 32.041N 103.679E   | 30.83–16.902                  | Abies spp.      | Wang and Wang (2013) | Inside area of stability at LGM Yes (Yes)                                    |
| 2–13 | Lugu Lake, Yunnan Province     | 27.667N 100.800E   | 22.77–21.86                   | Abies spp.      | Liao (2017)      | Inside area of stability at LGM Yes (Yes)                                    |
| 2–14 | Songpinggou, Sichuan Province  | 32.050N 103.670E   | 20.18–19                      | Abies spp.      | Mao (2011)       | Inside area of stability at LGM Yes (Yes)                                    |
| 2–15 | Beihai Lake, Tengchong, Yunnan Province | 25.830N 98.750E | 32–15                          | Abies spp.      | Bao (2010)       | Inside area of stability at LGM Yes (Yes)                                    |
| 2–16 | Tushi Lake, Tibet              | 28.810N 85.586E    | 20                            | Cyperaceae, Artemisia spp., fern | Yu (2008)      | Outside area of stability at LGM Yes (Yes)                                   |
| 2–17 | Dayanggou, Gansu Province      | 35.397N 103.913E   | 35–17                         | Pinus spp., Picea spp., Artemisia spp. | Wu et al. (1985) | Outside area of stability at LGM Yes (Yes)                                   |
| 2–18 | Xiaowangou, Tongwei, Gansu Province | 35.278N 105.446E | 20.714–10                     | Polypodiaceae, Pinus spp., Picea spp., Lycopodium japonicum Thunb. ex Murray, Chenopodiaceae | Wu et al. (1985) | Outside area of stability at LGM Yes (Yes)                                   |
| 2–19 | Landigou, Tongwei, Gansu Province | 35.201N 105.578E | 23.783–15.135                 | Polypodiaceae, Pinus spp., Picea spp., Chenopodiaceae | Wu et al. (1985) | Outside area of stability at LGM Yes (Yes)                                   |
| 2–20 | Jingning, Gansu Province        | 35.500N 105.833E   | 23.4–14.6                     | Cupressaceae, Zygophyllaceae, Compositae, Gramineae, Chenopodiaceae, Polygonaceae, Ranunculaceae, Ulmaceae | Tang et al. (2007) | Outside area of stability at LGM Yes (Yes)                                   |
| 2–21 | Fu County, Shaanxi Province    | 36.000N 109.500E   | 73–10                         | Corylus spp., Quercus spp., Alnus spp., Quercus spp., Ulmus spp., Betula spp., Celtis spp., Oleaceae, Comus spp., Salix spp., Toxicodendron vernicifluum, Platyctarya strobilace, Pinus spp., Picea spp., Tsuga spp. | Li and Ke (2006) | Outside area of stability at LGM Yes (Yes)                                   |
| 2–22 | Renacuo Lake, Gaize, Tibet     | 32.833N 84.250E    | 33.4–10.6                     | Pinus spp., Ulmus spp., Picea spp., Juglans spp., Betula spp., Cedrus spp., Artemisia spp., Humulus spp., Selaginella spp., Microlepia spp., Ephedra spp., Corylus spp. | Li (2014)       | Outside area of stability at LGM Yes (Yes)                                   |
| 2–23 | Milin, Tibet                   | 29.216N 94.213E    | 23–18                         | Pinus spp.      | Pan et al. (2013) | Outside area of stability at LGM Yes (No)                                    |

(Continues)
| Code | Site name | Latitude | Longitude | Estimated chronology (kyr BP) | Site type | Reference | Model prediction | Match between model by CCSM (MIROC) and data |
|------|------------|----------|-----------|------------------------------|----------|-----------|------------------|-----------------------------------|
| 2–24 | Huangheyuan, Qinghai Province | 34.700N 97.500E | 28–8 | Chenopodiaceae, Gramineae, Tamaricaceae | Han et al. (2011) | Outside area of stability at LGM | Yes (Yes) |
| 2–25 | Qiao County, Jingning, Gansu Province | 35.500N 105.833E | 44–11 | Pinus spp., Picea spp., Abies spp., Tsuga spp., Larix spp., Betula spp., Quercus spp., Ulmus spp., Artemisia spp., Pyrosia spp., Selaginella spp., Selaginella sinensis, Hicriopteris spp., Microlepria spp., Acer spp., Juglans spp., Salix spp. | Li et al. (2006) | Outside area of stability at LGM | Yes (Yes) |
| 2–26 | Gasikule Salt Lake, Qinghai Province | 38.085N 90.938E | 30–20 | Moraceae, Tamaricaceae, Actinidiaceae, Scrophulariaceae, Gramineae, Chenopodiaceae, Compositae, Leguminosae, Ranunculaceae, Thalictrum, Solanaceae, Rosaceae, Berberidaceae, Convovulaceae, Labiatae, Caryophyllaceae, Cruciferae, Cyperaceae, Polypodiaceae | Ye et al. (2013) | Outside area of stability at LGM | Yes (Yes) |
| 2–27 | Jiuquan, Gansu Province | 39.720N 99.370E | 16 | Pinus spp., Picea spp. | Shen (2008) | Outside area of stability at LGM | Yes (Yes) |
| 2–28 | Duantouliang, Tengger Desert, Gansu Province | 37.500N 104.8E | 28–23 | Betula spp., Artemisia spp., Juniperus spp., Pinus spp., Quercus spp., Salix spp., Rosa spp., Hippophae | Ma et al. (1998) | Outside area of stability at LGM | Yes (Yes) |
| 19 | Hongyuan region, Zoige Plateau, Sichuan Province | 32.788N 102.527E | 7.4–5.0 | Abies spp. | Wang et al. (2006) | Inside area of stability at mid-Holocene | Yes (Yes for Tmin area) |
| 20 | Arming River Basin, Western Sichuan Province | 28.275N 102.167E | 10.3–4.1 | Abies spp. | Cheng et al. (2010) | Inside area of stability at mid-Holocene | Yes (Yes) |
| 21 | Heqing Basin, Yunnan Province | 25.850N 100.483E | 6.98 | Abies spp. | Xiao et al. (2006) | Inside area of stability at mid-Holocene | Yes (Yes) |
| 22 | Butuo County, Southwestern Sichuan Province | 27.717N 102.867E | 8.6–4.0 | Abies spp. | Liu et al. (2003) | Inside area of stability at mid-Holocene | Yes (Yes) |
| 23 | Lugu Town, Mianning County, Sichuan Province | 28.283N 102.183E | 6 | Abies spp. | Cheng (2010) | Inside area of stability at mid-Holocene | Yes (Yes) |
| 24 | Yihai, Mianning County, Sichuan Province | 28.700N 102.183E | 5 | Abies spp. | Chen (1985) | Inside area of stability at mid-Holocene | Yes (Yes) |
| 25 | Lugu Lake Watershed, Yunnan Province | 27.667N 100.800E | 7–5 | Abies spp. | Zhang et al. (2016) | Inside area of stability at mid-Holocene | Yes (Yes) |
TABLE 1 (Continued)

| Code | Site name                                 | Latitude longitude | Estimated chronology (kyr BP) | Site type                                                                 | Reference               | Model prediction     | Match between model by CCSM (MIROC) and data |
|------|------------------------------------------|--------------------|-------------------------------|---------------------------------------------------------------------------|-------------------------|----------------------|---------------------------------------------|
| 26   | Lake Rukche area, Gorkha Himal, Central Nepal | 28.296N 84.776E    | 7.8–2.75                      | Humid oak forests with demanding elements dominated the vegetation cover | Schrötz and Zech (2004) | Outside area of stability at mid-Holocene | No (No)                                    |
| 27   | Analong County, Sichuan Province          | 25.167N 105.157E   | 5.99                          | *Pteris cratica*, *Dipteris conjugata*, *Pyrosetia lingua*, *Polypodium nipponica*, *Aleuritopteris pseudofarinosa*, *Keteleeria fortunei*, *Taxodium distichum*, *Adiantum Capillus veneris* | Mao (1991)              | Outside area of stability at mid-Holocene | Yes (Yes)                                  |
| 28   | Fanjing Mountain, Guizhou Province        | 27.786N 108.560E   | 5.53                          | *Cyclobalanopsis glauca*, *Quercus spp.*, *Castanopsis spp.*, *Betulaceae*, *Polypodiaceae*, *Athyriaceae* | Chen (1989)             | Outside area of stability at mid-Holocene | Yes (Yes)                                  |
| 29   | Shillong Village, Caohai Town, Weining County, Bijie City, Guizhou Province | 26.800N 102.167E   | 6.0–4.8                       | *Picea asperata*, *Tsuga chinensis*, *Salix spp.*, *Pinus spp.*, *Quercus spp.*, *Cyclobalanopsis glauca*, *Athyrium filix-femina*, *Aleuritopteris pseudofarinosa*, *Lycopodium japonicum* | Chen (1987)             | Outside area of stability at mid-Holocene | Yes for Tmax area (No)                      |
| 30   | Zoige Plateau, Sichuan Province           | 34.083N 102.167E   | 6.42–3.79                     | Cyperaceae, Gramineae, Asteraceae, Equisetaceae, Ranunculaceae, *Pinus spp.*, *Oleaceae*, *Betula spp.*, *Quercus spp.*, *Castanopsis spp.* | Guo et al. (2012)       | Outside area of stability at mid-Holocene | Yes for Tmax area (Yes)                     |
| 31   | Shangri-la County, Yunnan Province        | 27.817N 99.700E    | 5.5                            | *Blechnum orientale*, *Dipteris conjugata*, *Hicriopteris glauca*, *Gymnotheca involucrata*, *Acorus calamus*, *Mimosa pudica*, *Tamarix chinensis*, *Cupressus duclouxiana*, *Platycladus orientalis*, *Betula platyphylla*, *Ginkgo biloba*, *Rhapis excelsa*, *Vitex negundo* | Shi (2012)              | Outside area of stability at mid-Holocene | No (No)                                    |
| 32   | Guanzhai Village, Zhijin County, Bijie City, Guizhou Province | 26.769N 105.897E   | 6.71                          | *Pinus spp.*, *Aleuritopteris pseudofarinosa*, *Artemisia spp.*          | Zhu and Li (1994)       | Outside area of stability at mid-Holocene | Yes (Yes)                                  |
| 33   | Waqie Town, Hongyuan County, Sichuan Province | 33.150N 102.850E   | 8.512–5.000                   | Meadow                                                                    | Huang et al. (2012)     | Outside area of stability at mid-Holocene | Yes for Tmax area (No)                      |
| 34   | Chengdu Plain, Sichuan Province           | 30.500N 103.000E   | 4                             | Abies spp.                                                                | Luo et al. (2008)       | Inside area of stability at mid-Holocene | Yes (Yes)                                  |
| 35   | Mianning Area, Sichuan Province           | 29.000N 102.167E   | 8.8–5.0                       | Abies spp.                                                                | Dong et al. (2000)      | Inside area of stability at mid-Holocene | No (Yes)                                   |
| 36   | Xiaohaizi, Leibo, Sichuan Province        | 28.412N 103.781E   | 9.0–5.3                       | Abies spp.                                                                | Liu et al. (2004)       | Inside area of stability at mid-Holocene | Yes (Yes)                                  |
| Code  | Site name                     | Latitude/longitude | Estimated chronology (kyr BP) | Site type       | Reference† | Model prediction | Match between model by CCSM (MIROC) and data |
|-------|------------------------------|--------------------|-------------------------------|----------------|------------|------------------|---------------------------------------------|
| 2–29  | Heqing, Yunnan Province      | 26.573N 100.128E   | 6.98                          | Abies spp.     | Xiao et al. (2006) | Inside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–30  | Heihe farm, Zoige Plateau, Sichuan Province | 33.906N 102.536E | 9–3                           | Abies spp.     | Liu et al. (1995) | Inside area of stability at mid-Holocene | Yes for Tmin area (Yes for Tmin area)       |
| 2–31  | Zoige Plateau, Sichuan Province | 33.773N 102.550E | 6.46                          | Abies spp.     | Cai (2008)  | Inside area of stability at mid-Holocene | Yes for Tmin area (Yes for Tmin area)       |
| 2–32  | Hongyuan peatland, Sichuan Province | 32.778N 102.517E | 11.5–3                        | Abies spp.     | Zhou et al. (2011) | Inside area of stability at mid-Holocene | Yes (Yes for Tmin area)                    |
| 2–33  | Heqing, Dali County, Yunnan Province | 26.564N 100.175E | 6.98                          | Abies spp.     | Xiao et al. (2006) | Inside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–34  | Dawan, Gansu Province         | 34.800N 105.915E   | 9.5–7.5                       | Abies spp.     | Tang and An (2007) | Inside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–35  | Lantian, Shaanxi Province     | 34.152N 109.324E   | 5                             | Abies spp.     | Li and Sun (2005)  | Inside area of stability at mid-Holocene | Yes for Tmin area (Yes for Tmin area)       |
| 2–36  | Anlong County, Guizhou Province | 25.233N 105.355E | 5.99                          | Pinus spp., Gramineae, Keteleeria spp., Cupressus spp. | Mao (1991)  | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–37  | Fanjing Mountain, Guizhou Province | 27.786N 108.560E | 5.53–0.16                     | Gramineae, Polypodiaceae, Athyriaceae, Sinopteridaceae, Cyperaceae, Gramineae, Sinopteridaceae, Polyopodiaceae, Athyriaceae | Chen (1989) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–38  | Dadiwan, Longzhong, Gansu Province | 35.000N 105.915E | 8.2–4.3                       | Ulmus pumila L., Quercus spp., Betulaceae | Wei et al. (2009) | Outside area of stability at mid-Holocene | Yes for Tmax area (No)                      |
| 2–39  | Sujiawan, Gansu Province      | 35.539N 104.526E   | 8.2–4.3                       | Ulmus pumila L., Quercus spp., Betulaceae | Wei et al. (2009) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–40  | Landigou, Tongwei County, Gansu Province | 35.201N 105.578E | 15.135–0                     | Pinus spp., Rosaceae, Labiatae, Malvaceae | Wu et al. (1985) | Outside area of stability at mid-Holocene | Yes for Tmax area (Yes for Tmax area)       |
| Code | Site name                          | Latitude longitude | Estimated chronology (kyr BP) | Site type                                                                 | Reference | Model prediction | Match between model by CCSM (MIROC) and data |
|------|-----------------------------------|--------------------|-------------------------------|----------------------------------------------------------------------------|-----------|------------------|---------------------------------------------|
| 2–41 | Majiacha, Dingxi County, Gansu Province | 35.563N 104.654E  | 7.823–7.663                  | *Pinus* spp., *Chenopodiaceae*, *Ephedraceae*, *Compositae*, *Polypodiaceae* | Wu et al. (1985) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–42 | Xishuangbanna, Yunnan Province     | 22.001N 100.837E   | 7.25–0                       | *Pinus* spp., *Podocarpus* spp., *Dacrydium* spp., *Terminalia* spp., *Homonoia* spp., *Lithocarpus* spp., *Castanopsis* spp., *Alnus* spp., *Ilex* spp., *Quercus* spp., *Liquidambar* spp., *Fagus* spp., *Carya* spp., *Casuarina* spp., *Trema* spp., *Pterocarya* spp., *Rhioptelea* spp., *Apodytis* spp., *Tilia* spp., *Engelhardia* spp., *Gleditsia* spp., *Duabanga* spp., *Erythrina* spp., *Bridelia* spp., *Phyllanthus* spp., *Malolothus* spp., *Cephalanthus* spp. | Xu et al. (1998) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–43 | Yan’an, Shaanxi Province           | 36.585N 109.490E   | 8.13–4.37                    | *Pinus* spp., *Gramineae*, *Ranunculaceae*                                | He et al. (2000) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–44 | Qilian Mountain, Qinghai Province  | 38.202N 102.772E   | 7–6.3                        | *Picea* spp., *Sabina* spp.                                               | Zhu et al. (2001) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–45 | Fanjing Mountain, Guizhou Province | 27.940N 108.614E   | 10.0–8.1                     | *Symplocaceae*, *Cyperaceae*, *Gramineae*, *Chenopodiaceae*, *Compositae*, *Caryophyllaceae*, *Polygonaceae*, *Ranunculaceae*, *Rosaceae*, *Balsaminaceae*, *Cruciferae*, *Labiatae*, *Geraniaceae*, *Typhaceae*, *Athyriaceae*, *Polypodiaceae*, *Sinopteridaceae*, *Dennstaedtiaceae*, *Pteridaceae*, *Vittariaceae* | Chen et al. (1992) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–46 | Huining County, Gansu Province     | 35.859N 105.007E   | 5–0                          | *Betula* spp., *Quercus* spp., *Pinus* spp.                               | Liu (1992) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–47 | Tanggula Mountain, Tibet           | 34.214N 92.437E    | 11–4                         | *Pinus* spp., *Picea* spp., *Alnus* spp., *Castanea* spp., *Ulmus* spp., *Artemisia* spp., *Ephedra* spp., *Chenopodium* spp., *Dianthus* spp., *Sparganium* spp. | Wu et al. (2006) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |
| 2–48 | Wuda, Dangxiong, Yunnan Province   | 30.507N 91.240E    | 9–4                          | *Humulus* spp., *Quercus* spp., *Corylus* spp., *Rhododendron* spp., *Artemisia* spp., *Sensu* spp., *Cyperaceae*, *Liliaceae*, *Labiatae*, *Oleaceae* | Wang et al. (1981) | Outside area of stability at mid-Holocene | Yes (Yes)                                   |

Note: Numbers refer to localities shown in Figures S4 and S5.

*aAll references of this table are shown in Appendix S1.*
FIGURE 2  Predicted potential distribution of the four Abies taxa across the Tibetan Plateau based on current climate (a) A. forrestii, (b) A. fargesii var. faxoniana, (c) A. forrestii var. georgei, and (d) A. recurvata.
and A. forrestii var. georgei ca. 21 kyr BP are also well conveyed in the results. A relatively stable temperature range and heavier precipitation (Tables S4 and 3) strongly affected the aforementioned Abies distributions (Figures 3 and S3), allowing their extension from glacial refugia with an inclination toward shifting to higher latitudes. Yet, this expansion was mostly constrained over the LIG, which indicated that the warm period could have featured unfavorable climatic conditions for these two Abies species (Figures 3 and S3).

The stability surfaces steadily predicted an area extending along the central corridor of the A. forrestii and A. forrestii var. georgei distributions, and stretching from the eastern edge of the Salween River, northwards to the western edge of the Yangtze River (Figure 3), hereon referred to as the Heqing refuge (Figures 1 and 3). Habitable areas of A. forrestii and A. forrestii var. georgei were observed in the southern Hengduan Mountains area, where currently there are no A. forrestii and A. forrestii var. georgei trees occurring.

Unlike above, the distribution of A. recurvata since the mid-Holocene stretched to the adjacent mountain chains west of the Hengduan Mountains, and spread to the northeastern edge of the Longmen chain (Figures 1‒3 and S3). This contrasted with the distribution of A. fargesii var. faxoniana, which had shrunk and shifted somewhat northwards during the LGM (Figures 3 and S3, Table 2). When compared with the LGM, A. fargesii var. faxoniana displayed a wider and continuous potential distribution area for the present and the mid-Holocene. In general, the model showed suitable habitats occurring in areas toward both the northern and western parts of the Hengduan Mountains area. A refugial area of A. fargesii var. faxoniana and A. recurvata was inferred, occurring in the north of Sichuan Province, and referred to hereon as the Longmen refuge (Figures 1 and 3). However, much of this Longmen refuge area, which is now forested, was not projected as a suitable area for forests under 120–140 kyr BP prevailing environments, regardless of the forest characterization used (Figures 2, 3 and S3). Therefore, this area was not inferred to have maintained a considerable steady habitat area for A. fargesii var. faxoniana and A. recurvata, but rather to have served as temporary refuge only for these two taxa.

3.3 | Fossil and phylogeographic records

A classification of the fossils and pollen is given in Table 1. Concurrence and spatial constituencies were found between the potential distribution and pollen records of Abies species across the TP (Figures S4 and S5; Table 1). Overall, the pollen of Abies species

**FIGURE 3** Precited potential distribution for the four Abies during the mid-Holocene and LGM under two general circulation models (CCSM and MIROC) and LIG: (a) Abies forrestii, (b) A. fargesii var. faxoniana, (c) A. forrestii var. georgei, and (d) A. recurvata. The area surrounded by the red circle is Heqing refuge. The area surrounded by the blue circle is Longmen refuge. Refer Figure S3 for more information regarding the potential distribution of Abies at Tmax (maximum training sensitivity and specificity) and Tmin (minimum training presence) logistic thresholds.
TABLE 2  General distributional information of the four Abies (A. forrestii, A. faxoniana, A. forrestii var. georgei, and A. recurvata) as shown in the maps of Figures 2, 3, and S3

| Specie          | Type                      | S suitable (≥0.8) area (km²) | A Suitable (≥0.6, <0.8) area (km²) | B Suitable (≥0.4, <0.6) area (km²) | C Suitable (≥0.2, <0.4) area (km²) | Total (≥0.2) area (km²) | Suitable area (km²) | Tmin   | Tmax   |
|-----------------|---------------------------|------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|------------------------|---------------------|--------|--------|
| A. forrestii    | Present                   | 19                           | 48,056                            | 127,222                           | 155,630                           | 330,927                | 575,193             | 506,963 | 479,717 |
|                 | Mid-Holocene-CCSM4        | 8                            | 33,069                            | 114,477                           | 152,431                           | 299,985                | 554,217             | 545,815 | 479,717 |
|                 | LGM-CCSM4                 | 0                            | 17,896                            | 115,218                           | 160,892                           | 294,006                | 655,833             | 545,815 | 45,001  |
|                 | LIG                        | 0                            | 0                                | 5,827                             | 5,827                             | 5,827                  | 65,281              | 45,001  |        |
|                 | LGM-MIROC-ESM             | 0                            | 0                                | 0                                 | 0                                 | 0                      | 65,281              | 45,001  |        |
|                 | Mid-Holocene-MIROC-ESM    | 962                          | 40,859                            | 18,158                            | 108,716                           | 127,119                | 376,521             | 307,458 |        |
|                 | A. fargesii var. faxoniana| Present                     | 2                                | 17,371                            | 86,993                            | 156,088                | 260,454             | 437,243 |        |
|                 | Mid-Holocene-CCSM4        | 6                            | 9,600                             | 47,374                            | 90,092                            | 147,072                | 886,447             | 304,109 |        |
|                 | LGM-CCSM4                 | 0                            | 2,499                             | 23,430                            | 85,783                            | 111,712                | 1,003,468            | 293,912 |        |
|                 | LIG                        | 12,555                       | 59,971                            | 105,214                           | 205,662                           | 383,402                | 1,418,397            | 706,712 |        |
|                 | LGM-MIROC-ESM             | 6,801                        | 16,282                            | 35,767                            | 117,939                           | 176,789                | 1,137,294            | 376,207 |        |
|                 | Mid-Holocene-MIROC-ESM    | 548                          | 13,287                            | 30,093                            | 81,242                            | 125,170                | 684,203             | 221,859 |        |
| A. forrestii var.| Present                   | 227                          | 38,637                            | 125,680                           | 133,350                           | 297,894                | 847,235             | 413,867 |        |
|                 | Mid-Holocene-CCSM4        | 0                            | 29,550                            | 127,711                           | 117,458                           | 274,719                | 907,786             | 405,188 |        |
|                 | LGM-CCSM4                 | 340                          | 38,778                            | 123,381                           | 153,810                           | 316,309                | 1,164,859            | 502,603 |        |
|                 | LIG                        | 6                            | 9,529                             | 38,073                            | 57,439                            | 105,047                | 598,437             | 180,265 |        |
|                 | LGM-MIROC-ESM             | 452                          | 4,094                             | 51,403                            | 167,095                           | 223,044                | 1,093,381            | 432,592 |        |
|                 | Mid-Holocene-MIROC-ESM    | 206                          | 43,653                            | 101,185                           | 136,557                           | 281,601                | 1,154,214            | 458,615 |        |
| A. recurvata    | Present                   | 1,506                        | 7,412                             | 17,444                            | 70,318                            | 96,680                 | 212,514             | 204,202 |        |
|                 | Mid-Holocene-CCSM4        | 54                            | 2,489                             | 7,498                             | 26,551                            | 36,592                 | 92,329              | 88,000  |        |
|                 | LGM-CCSM4                 | 0                            | 1,857                             | 5,792                             | 23,387                            | 31,036                 | 102,615             | 95,272  |        |
|                 | LIG                        | 0                            | 0                                 | 0                                 | 0                                 | 0                      | 942                 | 587     |        |
|                 | LGM-MIROC-ESM             | 3,875                        | 10,539                            | 27,265                            | 63,618                            | 105,297                | 255,833             | 245,404 |        |
|                 | Mid-Holocene-MIROC-ESM    | 61                            | 1,551                             | 3,174                             | 9,675                             | 14,461                 | 37,085              | 35,057  |        |
applied throughout the entire eastern TP, from the Hengduan Mountains to the Longmen Mountains, during the Quaternary period. However, at the LIG, the distribution area of Abies almost disappeared entirely from the northern regions of the TP (Figures 3 and S3 and S5).

Unfortunately, at the LIG, only three pollen locations (Heqing Basin, Kunming Basin, Yunnan Province) were able to convey the status of the Abies populations in the TP. Hence, the Abies refugia during this period cannot be understood well on the basis of paleo-aphylogeographic evidence alone. Nonetheless, it should be noted that all 11 records agreed with the predictions made by the GCMs during the LIG according to Otto-Bliesner et al. (2006) (Figures S4 and S5).

Thirty-two pollen datasets representing the LGM (a period of 21 kyr BP) indicated an expansion of grassland vegetation and other non-Abies plants, which is in line with the predictions from the 21 kyr BP consensus map by the GCMs obtained through the CCSM4 simulation (Table 1, Figures 4 and S4). Only three records (codes 15-17) contradicted the predictions made by the CCSM4 simulation, which projected the occurrence of Abies in these regions, while six pollen datasets disagreed with projections made by the MIROC-ESM simulation. Therefore, the result of the MIROC-ESM simulation seems to overestimate the forest distribution over the 21 kyr BP period (Figures S4 and S5). The most outstanding fossil evidence was detected in Hongya County (code 5), Xiaohaizi County, and Leibo County (code 10) in the eastern Hengduan Mountains, areas that are located far from the current distribution of these four Abies taxa. This finding is of great significance in helping to understand the past distributions of Abies trees. Pollen investigations suggested that Abies taxa occupied mostly low-elevation mountain ranges, generally at the base of mountains during cold and dry times, when not undergoing fast expansion to nearby areas during the postglacial recovery. Taken together, these findings suggest that Abies persisted in refuges in the Heqing and Longmen areas during the last ice age.

The predictions obtained by combining the 6 kyr BP models produced by the GCMs through CCSM4 and MIROC-ESM simulations (Table 1; Figures S4 and S5) were inconsistent, as only two pollen records were available. The Hongyuan region, the Zoige Plateau, and Sichuan Province (code 19) are currently situated in the A. recurvata forest ecotone, indicating that the forest margin represented in Figure 3c during the mid-Holocene by the GCMs obtained via MIROC-ESM had gradually shifted northward. This proposition accords with the pollen and phylogeographic records at this location, reflecting an overall tendency of forest extension to have occurred during 6–10 kyr BP based on the available phylogeographic evidence.

Concerning the A. fargesii var. faxoniana and A. recurvata populations, those from the Longmen refugia exhibited higher cpDNA diversity compared with the nonrefugia areas situated at the south or west of the Longmen Mountains (Figure S6; Table S3). More details regarding the haplotype, haplotype diversity, and nucleotide diversity for each of the sampled locations are included in Table S3. Each of the aforementioned two taxa has a relatively high total genetic diversity (H1) and lower within-population diversity (H3), respectively. According to the PERMUY analysis, the N ST exceeded the G ST for

| Variable | Percent contribution (%) | Variable | Percent contribution (%) | Variable | Percent contribution (%) | Variable | Percent contribution (%) |
|----------|--------------------------|----------|--------------------------|----------|--------------------------|----------|--------------------------|
| TAR      | 28.0                     | PS       | 21.0                     | TAR      | 24.2                     | TDQ1     | 30.0                     |
| TWQ      | 13.6                     | PCQ      | 18.5                     | PHQ      | 22.9                     | MDR      | 23.3                     |
| Slope    | 13.4                     | TAR      | 15.8                     | TWQ      | 19.6                     | PHQ      | 16.9                     |
| PHQ      | 13.4                     | PHQ      | 15.3                     | MDR      | 11.9                     | Slope    | 11.3                     |
| TDQ      | 13.1                     | TDQ      | 12.3                     | TDQ      | 9.6                      | PS       | 9.9                      |
| PCQ      | 6.5                      | TDQ      | 12.3                     | Slope    | 3.9                      | TWQ      | 6.2                      |
| MDR      | 6.4                      | Slope    | 1.1                      | Pmax     | 3.1                      | PCQ      | 1.1                      |

Abbreviations: MDR, mean diurnal range; PCQ, precipitation of coldest quarter; PHQ, precipitation of warmest quarter; Pmax, precipitation of wettest month; PS, precipitation of seasonality; TAR, temperature annual range; TCQ, mean temperature of coldest quarter; TDQ, mean temperature of driest quarter; TWQ, mean temperature of wettest quarter.

FIGURE 4 Ordinate plot from redundancy analysis (RDA) on the four Abies change trends (red arrows) and their relationships with environmental variables (blue arrows). MDR, mean diurnal range; Pann, annual precipitation; PHQ/WCQ, precipitation of warmest/coldest quarter; PS, precipitation seasonality; TAR, temp annual range; TD, mean temp of driest quarter; Tmin, min temp of coldest month; TWQ/TDQ, mean temp of wettest/driest quarter.

TABLE 3 The top seven (relative basis) contributions of the environmental variables to the MaxEnt model

| Variable | Percent contribution (%) | Variable | Percent contribution (%) | Variable | Percent contribution (%) | Variable | Percent contribution (%) |
|----------|--------------------------|----------|--------------------------|----------|--------------------------|----------|--------------------------|
| TAR      | 28.0                     | PS       | 21.0                     | TAR      | 24.2                     | TDQ1     | 30.0                     |
| TWQ      | 13.6                     | PCQ      | 18.5                     | PHQ      | 22.9                     | MDR      | 23.3                     |
| Slope    | 13.4                     | TAR      | 15.8                     | TWQ      | 19.6                     | PHQ      | 16.9                     |
| PHQ      | 13.4                     | PHQ      | 15.3                     | MDR      | 11.9                     | Slope    | 11.3                     |
| TDQ      | 13.1                     | TDQ      | 12.3                     | TDQ      | 9.6                      | PS       | 9.9                      |
| PCQ      | 6.5                      | TDQ      | 12.3                     | Slope    | 3.9                      | TWQ      | 6.2                      |
| MDR      | 6.4                      | Slope    | 1.1                      | Pmax     | 3.1                      | PCQ      | 1.1                      |

Abbreviations: MDR, mean diurnal range; PCQ, precipitation of coldest quarter; PHQ, precipitation of warmest quarter; Pmax, precipitation of wettest month; PS, precipitation of seasonality; TAR, temperature annual range; TCQ, mean temperature of coldest quarter; TDQ, mean temperature of driest quarter; TWQ, mean temperature of wettest quarter.
each species, and a significant phylogeographical structure was detected for the A. fargesii var. faxoniana and A. recurvata populations (Table S3). Furthermore, Tajima’s D and Fu’s Fs tests of neutrality all produced significant negative values (Table S3). These outcomes indicate strong agreement between the observed and expected distributions. The elapsed times since the species extension were projected to be 1,542, and 8,086 kyr BP for A. fargesii var. faxoniana and A. recurvata, respectively.

3.4 | Environmental predictors of the studied Abies taxa

Estimates of the relative contribution (percentage) of each environmental predictor used to build Maxent models are presented in Table 3. The pluviometric-related variables (i.e., PS, PHQ, and PCQ), the thermometric variables (i.e., MDR, TAR, TWQ, and TDQ), and the topographic variables (i.e., slope) all significantly influenced the ENMs. Importantly, they could enhance our understanding of distribution patterns of the four endemic Abies taxa. The slope contributed very high gains (>1.0) when used alone for two Abies species (Figure S7), meaning that slope was important as climatic factors. However, the respective contributions of environmental variables to the four tree taxa were quite different (Figure S7). The Maxent model showed that TAR was the most significant variable for explaining the distribution of A. forrestii and A. forrestii var. georgei. TWQ and PHQ also played decisive roles in explaining the distribution model of A. forrestii and A. forrestii var. georgei. PS, by contrast, was the key variable explaining the distribution of A. fargesii var. faxoniana. However, the MDR of temperature and the TDQ were prominent in the distribution model of A. recurvata.

The RDA (Figure 4) revealed a clear distinction between the environmental requirements of the four Abies taxa, especially on the axes denoting climatic variables (temperature and rainfall), in contrast to the overlapping topographic features between the two habitats. This revealed the TAR and PHQ variables explained 29.0% of the variation in the trends of the four Abies taxa. The remaining environmental variables together explained 40.1% of the variation-species relationships expressed in the RDA model. Its unexplained residual variation may have resulted from integrated effects of other factors (e.g., soil type, land cover, and interspecific competition).

4 | DISCUSSION

4.1 | Model accuracy and prediction uncertainty

The calibrated potential distribution models for A. forrestii, A. fargesii var. faxoniana, A. forrestii var. georgei, and A. recurvata attained high AUC values (Figure S2), thus indicating all models had excellent performance (Raes et al., 2014). The modeling technique we used relied on a powerful method (Maxent) that deals strictly with species’ occurrence records (Elith & Leathwick, 2009; Phillips et al., 2006). The outcomes from these ENMs might be among the most accurate attainable for the used dataset (occurrence records and environmental data) (Raes et al., 2014). According to the values of the evaluation metrics used, the Maxent model under the CCSM4 simulation was more accurate than that under the MIROC-ESM simulation at the LGM and during the mid-Holocene for the study area. However, inaccuracies from paleoclimatic scenarios might have increased the uncertainty of these predictive models. For instance, issues could appear because of the appearance of dissimilar climatic settings when ENMs are projected across orthogonal gradients of climatic changes, specifically for those that happened during mid-Holocene period. In this case, modeling methods will have unfamiliar or erratic performance when used for prediction in those areas (Alba-Sánchez & López-Merino, 2010). More issues may have emerged as the GCMs’ model data could have undervalued the heating and precipitation fluctuations across the Tibetan Plateau (TP), particularly during the mid-Holocene period (Li, Wang, & Li, 2013). Therefore, the models presented here could have overestimated the Abies distribution during the LGM and the mid-Holocene (Tinner & Valsecchi, 2013). Yet overfitting should not be construed as low performance, because the models used climatic data alone to predict the potential distributions of the Abies taxa, consequently overlooking other contributing factors (e.g., soil type, land cover, and interspecific competition; Wang, Jia, Wang, Zhua, & McDowell, 2017) that might have been involved in shaping the pattern of distributions; this was clearly suggested by the PCA and RDA results (Figures S1 and 4). The spatial resolution of the applied models may have posed an additional constraint, mostly in those regions with intricate topography (Adhikari, Barik, & Upadhaya, 2012). Finally, the local climate may vary greatly from the climate actually being simulated in the corresponding grid box of the models. Improving the models’ resolution through explicit consideration of environmental predictors with higher resolution should enhance the depiction of the studied region (Alba-Sánchez & López-Merino, 2010). Moreover, the overpredictions of the models for A. forrestii and A. forrestii var. georgei in the western area (Himalaya Mountains area) for the LGM and the mid-Holocene could be explained by the limited rate of species proliferation. Likewise, in the eastern area of Guizhou Province in the LGM and mid-Holocene, the overpredictions found there are consistent with its geographic structures possibly acting as plant dispersal barriers (Richards & Bock, 1973; in the case of this research: north-south directional Hengduan Mountains).

4.2 | Abies distribution and refugia based on ENMs, paleorecords, and phylogeography

By combining ecological niche characteristics derived from the environmental characteristics of identified records of Tibetan endemic Abies taxa with their paleoecological investigations, we obtained a more refined depiction of the distribution, discontinuities, and segregation among these tree taxa. This will help provide a greater understanding of the ecology and climatic niche of
Abies taxa and could also contribute to improving relevant climate change mitigation strategies. At the LIG, the combined effects of increasing fluctuations of temperature and precipitation throughout the TP (see Table S4) resulted in a contraction and disintegration of the Abies populations (Figures 3 and S3, Table 2). However, these events did not reach the level of severity that would lead to total extinction of the Abies taxa. Notably, topography was a critical factor, and this could have driven the shifting of tree populations in the basins rather than in the plains or mountains, albeit under a stable climate (Willis & McElwain, 2002), when seeking to persist and avoid extirpation. Thus, the Heqing Basin region, in addition to providing refugia for other species (Du et al., 2017), had sufficient topographical heterogeneity to provide many suitable microhabitats for the persistence of A. forrestii and A. forrestii var. georgei. Geographical overlapping among the Abies taxa was widespread throughout the glacial and interglacial times (Du et al., 2017).

During the LGM, the collective effects of reduced annual precipitation and lower summer and winter temperatures across the TP (Table S4) resulted in a shortened growing season and lowered level of atmospheric CO₂, down to 200 ppm (Braconnot et al., 2007). In addition, and most remarkably, it apparently caused the contraction and fragmentation of A. fargesii var. faxoniana and A. recurvata populations (Figure 3; Table 3). Conversely, the other two Abies taxa expanded their populations in this area during the same period, because smooth fluctuations of temperature and precipitation were more important for them than were changes in other environmental variables (Table 3). Analogous results have been reported for two other tree species at the TP, Taxus wallichiana and Quercus aquifolioides (Du et al., 2017; Yu, Zhang, Gao, & Qi, 2014). In the Northern Hemisphere, particularly in East Asia and western North America, the movement and shift of northern Abies taxa southward to the glacial region and the migration of southern Abies taxa northward to the interglacial region have been reported (Alba-Sánchez & López-Merino, 2010; Terhürne-Berson, Litt, & Cheddadi, 2004). Our results contradict that finding, since during the LGM all four endemic Abies taxa gradually receded from south to north in the TP. This process of receding may have been caused by Quaternary climatic fluctuations (Xiang et al., 2007). Extensive climatic changes characterized the Quaternary, which involved the repeated development and retreat of glaciers with sporadic warming periods (Owen, 2009). Such a transformation could have created various habitats where the Abies species migrated to find niche locations in the TP, whenever the global climate became colder or warmer (Cao et al., 2015). Additionally, the plateau uplifting has formed a natural separation between the temperate and subtropical zones. Further, it would have been difficult for cold air from Siberia and warm humid air from the Pacific Ocean to infiltrate to the central part of the southeastern TP, as the mountains acted as a barrier during the glaciations. In this way, a receding pattern of Abies taxa formed from south to north along the TP. Liang et al. (2018) also revealed numerous montane species in the Hengduan Mountains shift to higher elevations not only northward but also westward. The plateau uplifting and climatic fluctuations during the Quaternary overwhelmingly influenced the endemic biome, which shifted from south to north and was associated with glaciation in the late Pleistocene period (Zhang et al., 2000). In parallel, topography was a crucial factor in setting and identifying the range within which populations could expand unimpeded along the continuous mountain ranges (Xiang et al., 2006). In this respect, the Longmen and Hengduan Mountains ranges provided sufficient topographical variability for Abies to spread into other regions during the LGM (Figure 3).

During the mid-Holocene, an extension of the Abies taxa populations is well reverberated by their present outcomes, in that those endemic Abies taxa displayed larger and continuous potential distribution areas relative to those at the LIG and LGM (see Figure 3). The increased precipitation and warming (Table S4) would have allowed A. fargesii var. faxoniana, A. forrestii, and A. forrestii var. georgei to spread; however, A. recurvata relied less on precipitation for its expansion since the last glacial period (Wang, Xu, et al., 2017). Their areas of habitation, as well as their spread with increasing elevation in the mountainous regions, are features very similar to the contemporary distribution of these taxa. By comparing and relating the three predictions (current ENM, mid-Holocene ENM, and LGM ENM), we found that the reconstructed distribution patterns differed significantly for each Abies taxa, this finding perhaps reflecting the varied responses of each taxa to differing environmental variables (see Figures 2, 3, 4, and S3; Tables 2 and 3).

The ENMs yielded at least four well-differentiated distribution ranges for the related Tibetan Abies species (Figures 2 and 3): A. fargesii var. faxoniana occurred in the Longmen and Daba Mountains, the range of A. recurvata was distributed in the Longmen Mountains and the Yangtze River Basin at the LGM, and both A. forrestii and A. forrestii var. georgei were found along the Heqing Basin during the LIG. Previous studies (e.g., Zhan, 2011) have suggested that western Sichuan Province was probably a refuge for Abies taxa since the LIG. The overlap observed between past Abies refugia, as drawn from the fossil-pollen accounts, and the potential distributions of its taxa provide new insights into how Abies species were distributed across the TP during the Quaternary period. The palynological data provided evidence for an established ecologically steady area in which conditions safeguarded the residual Abies populations, maintaining their survival in the face of the extreme effects arising from the drastic Quaternary climate oscillation. Niche conservatism has been documented throughout the present-day distributions of A. forrestii and A. forrestii var. georgei (Figures 2, 3, and S4). For the LIG, it was revealed that the area where Abies populations had existed extended into the Heqing region and this area corresponded to the presumed refugia (Table 1; Figure 4). This area is considered as a major refugia of Quaternary glaciation for various tree species, namely Taxus wallichiana, Quercus aquifolioides, Picea likiangensis, Dipentodon, and Primula secundiflora (Du et al., 2017; Gao et al., 2007; Yu et al., 2014). The most divergent hotspot of A. fargesii var. faxoniana and A. recurvata was the Longmen area, where both species harbored high levels of genetic diversity (Figure S6), and the spread of their populations is
supported by the significant negative values obtained for all neutrality assessments (Tajima’s D; Fu’s Fs). We determined that a sudden population expansion for *A. fargesii* var. *faxoniana* and *A. recurvata*, respectively, began ca. 11,542 and 8,086 years ago, in the Longmen Mountains area.

By also considering the indicators of genetic diversity and nucleotide diversity (Zhan, 2011), the populations of *A. fargesii* var. *faxoniana* that attained a high h value and a low Pi value had probably experienced an expansion in their distribution following a long-standing period of suffering from a low effective population size. Accordingly, all of these outcomes converge in supporting the hypothesis that both *A. fargesii* var. *faxoniana* and *A. recurvata* populations at the Longmen areas have expanded (Figure S6). The Longmen Mountains, however, were not projected to have retained an extensive area offering stable habitat for *A. fargesii* var. *faxoniana* and *A. recurvata*, but rather it served as a temporary refuge for both tree species only at the LGM.

**4.3 | Ecological variables affecting the distributions of the four related *Abies* taxa**

The four related *Abies* taxa differed significantly in their climatic niche dimensions (Figure 4). This result is consistent with climate variables driving the distribution strategies of closely related plant species; that is, mean temperature of the coldest quarter significantly impacted the distribution of vegetation type (Wang, Xu, et al., 2017) and the minimum temperature of the coldest month was the main limiting factor for the growth of coniferous temperate forests in southwest China (Li, Peng, & Higa, 2016). In contrast, it was reported that *Abies* species were cold-tolerant, hydrophilic, sensitive to high temperature, and intolerant to aridity (Wang, Jia, et al., 2017). Such inconsistent results may arise from differences in the adaptation strategies of endemic *Abies* species to the environmental variables (Table 3; Figure S7). Also, divergent and convergent strategies might lead to an over- or underestimation of the suitable distribution area for combinations of different co-occurring species, as noted by Willis and McElwain (2002) and Du et al. (2017). Our RDA suggested that *A. fargesii* var. *faxoniana* and *A. recurvata* were better capable of adapting to more magnitude of fluctuation in temperature and precipitation, while the other two taxa are adapted to the higher precipitation of the Eastern Tibetan Plateau (Figure 4). Still, the effect of temperature fluctuations on *Abies*’ distributions was greater than that of either increases or decreases in temperature alone (Table 3). This conclusion is consistent with the current distribution of these four endemic *Abies* taxa: In the south, *A. forrestii* and *A. forrestii* var. *georgei* occur in wetter areas, while in the north, *A. fargesii* var. *faxoniana* and *A. recurvata* occupy an area of the TP that undergoes greater temperature magnitude of fluctuation (He et al., 2015; Wang, Jia, et al., 2017). Since most studies tend to focus on the impacts of climatic changes, they simulate increases in average temperature, thereby ignoring the effects of changes in magnitude of fluctuation of temperature (Gazol et al., 2015; Koo et al., 2017; Tinner & Valsecchi, 2013; Xiong et al., 2016). Our results suggest the importance of temperature fluctuations for affecting the growth and distribution of trees, and this variable should be considered when assessing the effects of future changes in climate on plant species. Slope is typically an important ecological factor that influences the distribution of local plant species (Adhikari et al., 2012). Consistent with other regional studies and investigations (Adhikari et al., 2012; Alba-Sánchez & López-Merino, 2010), we found that slope was an important contributor to the distribution of *Abies* taxa studied here across the TP.

**5 | CONCLUSIONS**

The strong agreement of paleorecords with our model predictions demonstrated the merit of using the Maxent modeling approach for projecting the distributions of endemic *Abies* taxa in the TP. The overall reconstructed distributions of the *Abies* taxa differed dramatically going from the late Pleistocene to the present. All the endemic *Abies* taxa at the TP exhibited a pattern in that they receded from south to north during the late Pleistocene. In the case of *A. fargesii* var. *faxoniana* and *A. recurvata*, the Longmen refuge served only as a temporary refuge for them since the LGM, whereas both *A. forrestii* and *A. forrestii* var. *georgei* were found distributed throughout the Heqing refuge since the LIG. The annual temperature range was the most important variable for explaining the distributions of *A. forrestii* and *A. forrestii* var. *georgei*. However, seasonal precipitation and the mean temperature of the driest quarter contributed significantly to the distribution model for *A. fargesii* var. *faxoniana* and *A. recurvata*, respectively. Further, the slope also contributed substantially to the above *Abies* distribution models. Varied adaptation strategies might well be the reason for differences found in the past and current potential distribution patterns of these four related *Abies* taxa at the TP. Incorporating ecological niche characteristics from *Abies* species combined with their paleoecological investigations provides a useful approach to better understand species migrations under climate changes. It could help guide rational management strategies of forests whose keystone species exist in high-altitude regions. Future work should focus on whether other endemic tree species (such as *Picea, Metasequoia*), used the same refuge as, for example, the Heqing refuge from this study.

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The contributing authors declare no conflict of interests regarding
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All authors worked together to design this study. Q.X. and F.Z.
collected the data. Q.X., M.A.D., and B.P. carried out the analysis.
Q.X., K.P., L.Z., and M.W.A.H. wrote the draft of this manuscript.
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DATA AVAILABILITY STATEMENT
All generated or analyzed data of this study are given in this pub-
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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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