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Climate change jointly with migration ability affect future range shifts of dominant fir species in Southwest China

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Abstract

Aim: As a prominent geographical distribution centre for the dark coniferous forests, mountains of Southwest China (MSWC) is experiencing an unprecedented warming trend, posing severe challenges to the survival of dominant fir (*Abies*) species. Although plant's migration ability is a prerequisite for its survival in changing environments, it has often been ignored in species distribution models (SDMs). This study aimed to quantify the magnitude and direction of range changes by the year 2080 for six dominant fir species, that is *Abies recurvata*, *Abies faxoniana*, *Abies squamata*, *Abies ernestii*, *Abies forrestii* and *Abies georgei*, with an emphasis on exploring the relationship between migration ability and projected distributions.

Location: The mountains of Southwest China.

Methods: We applied the Maximum Entropy (Maxent) algorithm to calibrate ecological niche models and to project the climatically suitable areas (CSAs) of each species under two emission scenarios (RCP 4.5 and RCP 8.5). Additionally, we delimited future species ranges by three migration scenarios (full-, no- and partial-migration scenarios).

Results: The simulations showed the distinctive responses of the six fir species to anthropogenic climate change (ACC). By 2080, the distribution areas of *Abies recurvata* were projected to decline only in the no-migration scenario but increase under the full- and partial-migration scenarios, while the other five species were projected to decline in the majority of emission × migration scenarios. Fir species in the southern region were predicted to be more vulnerable to ACC due to the larger losses in CSAs and a stronger effect of the partial-migration scenario on the newly colonized areas of this group. The studied species showed a simulated migration trend (northward and westward) to the interior Qinghai-Tibet Plateau under ACC.

Main conclusions: Benefits or losses for species under ACC depended on the geographical location, their ecological niches and migration abilities, which provide essential insights for a spatial conservation assessment of biodiversity hotspots in the future.

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KEYWORDS
Abies forest, climate change, migration ability, mountains of Southwest China, potential distribution, SDMs

1 | INTRODUCTION

The human influences on climate-changing are significant and are dominated by the emissions into the atmosphere of greenhouse gases (IPCC, 2013; Neukom et al., 2019; Ripple et al., 2017; Steffen et al., 2018). The resulting alterations in temperature and precipitation patterns are threatening the stability of forest ecosystems worldwide by affecting their ecophysiology, morphology, interspecific interactions and productivity (Eastman, Sangermano, Machado, Rogan, & Anyamba, 2013; Liu, Li, Li, & Motesharrei, 2015; Pecl et al., 2017). Driven by anthropogenic climate change (ACC), plants may change their phenological or physiological responses or migrate to more suitable habitats to avoid being affected by adverse climatic conditions; if these responses fail, plant species face the risk of extinction (Corlett & Westcott, 2013; Thomas et al., 2004; Walther et al., 2002). Numerous well-documented examples of plant migration due to ACC have been observed around the world (e.g. Davis & Shaw, 2001; Kelly & Goulden, 2008; Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008). On a global scale, ACC has dramatically altered the distribution of many species (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Scheffers et al., 2016).

For drawing some enlightenment into how future ACC will affect species distributions, conservationists have tried to figure out the effects of recent as well as historical climate fluctuations on species distributions through field observation (e.g. Kelly & Goulden, 2008; Zhu, Woodall, & Clark, 2012), palaeobotany (Jackson, Betancourt, Lyford, Gray, & Rylander, 2005; Liepelt et al., 2009) or molecular phylogeographical methods (e.g. McLachlan, Clark, & Manos, 2005; Naciri & Gaudeul, 2007). However, these approaches tend to concentrate on specific species at a small scale because of the costly and/or burdensome collection efforts. Moreover, the methods mentioned above are not sufficient for predicting the potential changes in species distributions under future ACC.

Species distribution models (SDMs) (also referred to as ecological niche models, ENMs, see Franklin, 2009; Peterson et al., 2011) quantify the relationship between existing occurrence records and environmental factors through multiple algorithms and then generate species habitat suitability (Guisan & Zimmermann, 2000). Benefitted by the simplicity of SDMs and data accessibility (Merow et al., 2014), researchers can generally estimate species' potential range shifts and threat levels under future ACC (Elith et al., 2011; Guisan & Zimmermann, 2000). Recently, a number of SDMs have been used to simulate range changes at intercontinental or regional scales in response to potential ACC, emphasizing pessimistic views about the survival of many species in the coming decades due to habitat loss (e.g. Assis, Araújo, & Serrão, 2018; Costion et al., 2015; Dyderski, Paź, Frelich, & Jagodziński, 2018; Ponce-Reyes et al., 2017; Rosenblad, Perret, & Sax, 2019; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005).

In the face of upcoming rapid climate change, it is unrealistic for plants to be able to evolve in correlation with physiological adaptation strategies in a short period, so the migration or dispersal ability is a prerequisite for their survival (Corlett & Westcott, 2013). However, since migration ability was not effectively taken into account in initial modelling (Guisan & Thuiller, 2005; Pearson & Dawson, 2003), the majority of SDM studies prefer to apply either full- or no-migration scenarios in predicting the species' potential distribution under future ACC (Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Bateman, Murphy, Reside, Mokany, & VanDerWal, 2013). In fact, the actual future distributions of species are likely to lie somewhere between the no- and full-migration scenarios (Berg et al., 2010). The forecasts from SDMs without considering a realistic migration ability of species may hinder our accurate judgement of the real risks to species, by either over- or underestimating them (Alexander et al., 2018). Recently, more researchers have become aware of this problem and have tried to use various modelling approaches to incorporate more realistic migration (i.e. partial-migration scenarios) into SDMs, for example, future projections for plants or animals in South Africa (Midgley, Hughes, Thuiller, & Rebelo, 2006; Uribe-Rivera et al., 2017), Australia (Fitzpatrick, Gove, Sanders, & Dunn, 2008; Reside, Vanderwal, & Kutt, 2012), and Europe (Meier, Lischke, Schmatz, & Zimmermann, 2012; Saltre, Duputie, Gaucherel, & Chuine, 2015). To some extent, in comparison to full-migration and no-migration scenarios, these predictions have improved the accuracy of modelling results.

Since the Quaternary period, the fluctuation in temperature between glacial and inter-/post-glacial periods induced a dramatic change in species distributions at the global scale (Hewitt, 2000). Fortunately, the mountains of Southwest China (MSWC) has served as refugia and enabled the survival of species during globally decreasing temperatures due to the relative stability of its local climate. The distribution of many species, for example *Juniperus przewalskii* (Zhang, Chiang, George, Liu, & Abbott, 2005), *Picea crassifolia* (Meng et al., 2007) and *Abies* species (Song et al., 2012) on the Qinghai-Tibet Plateau (QTP) is also closely related to the retreat or advancement of glaciers and the existence of refugia in MSWC. Additionally, mountains with a substantial elevation range offer short-distance corridors for the migration of species at a vertical gradient, and these species can recolonize when the temperature becomes more suitable again (Qiu, Fu, & Comes, 2011). Currently, the MSWC is experiencing an unprecedented warming trend, which is much higher than the global average warming trend over the past half-century, posing a severe challenge to the

survival of mountain plant communities (Alexander et al., 2018; Shi et al., 2015). Given the potential risks faced by species in the MSWC, it is necessary to simulate the distribution dynamics caused by ACC in advance.

Firs (*Abies*) are the dominant species of dark coniferous forests that are widely distributed in temperate and subtropical regions of the Northern Hemisphere (Fan, 2006; Farjon, 2001; Semerikova, Khrunyk, Lascoux, & Semerikov, 2018). The growth of these cold-tolerant and moisture-loving plants is based on strict requirements for temperature and humidity stability, so these plants are highly sensitive to ACC (Shi, 1996). The latest future projections of fir species worldwide based on SDMs generally have indicated an overall decline in their habitat area and a northward migration trend, such as in Europe (e.g. Dyderski et al., 2018; Gutiérrez Hernández, 2018; Thurm et al., 2018), North America (e.g. Sáenz-Romero, Rehfeldt, Duval, & Lindig-Cisneros, 2012) and East Asia (e.g. Chhetri, Gaddis, & Cairns, 2018). Throughout the temperate and cold temperate regions of Eastern Asia, dominant firs are keystone species to the functions of ecosystems, such as nutrient cycling (e.g. Duan, Dong, Zhang, Zhang, & Chen, 2014), water conservation (e.g. Ren, Hou, Ma, & Zha, 2017), carbon storage (e.g. Wang et al., 2014) and, above all, biodiversity maintenance (e.g. Lu et al., 2018; Qu et al., 2014). Therefore, many physiological and ecological experiments on these trees have been carried out under climate change (Duan et al., 2014; Guo, Zhang, Wang, Gu, & Liu, 2018; Shen, Zhang, Liu, & Luo, 2014; Wang et al., 2014).

To our knowledge, a few studies have compared current and future suitable habitats of firs in China at the genus level by SDMs, and they suggest that the ranges of firs will shrink and shift northward under future ACC (Liu, Wang, He, & Zhang, 2018; Shao, Zhang, Phan, & Xiang, 2017). Regrettably, when these SDMs were conducted, the influence of migration ability was ignored, and differences among species were masked by modelling the whole genus. Meanwhile, it is argued that plants in different regions will show individualized responses to ACC, depending on species-specific physiological tolerance (Lindner et al., 2014). Because of the strong inter-regional differences in topography, climate, vegetation and physical barriers, the feedback mechanism of plants to ACC in the MSWC is complex (Bellard et al., 2014). Therefore, there is an urgent need for a thoughtful future assessment of the multiple fir species of the MSWC, taking the interaction between migration limitation and climate change into account.

In the present study, we aimed to simulate climatically suitable areas (CSAs) and quantify the magnitude and direction of the changes in projected distributions of six fir species in the MSWC from the current period to 2061–2080 under different climate × migration scenarios. Due to the complex topography and climate conditions of the MSWC, we formulated three hypotheses: (I) assuming full migration, driven by different climatic factors, not all firs of this region will face a reduction in CSAs, and some may benefit from future climate change and obtain larger CSAs; (II) assuming partial migration, the predicted areas of newly colonized habitats of some fir species may be significantly reduced; and (III) not all species are expected to migrate northward in response to rapid future climate change. Considering these three hypotheses, we representatively selected six dominant fir species from different parts of the MSWC to predict current and project future habitat suitability using the Maximum Entropy (Maxent) model (Phillips, Anderson, & Schapire, 2006). Taking into account the uncertainty of future ACC, two emission scenarios, RCP 4.5 and RCP 8.5 (Meinshausen et al., 2011), were selected. In addition, we applied three migration scenarios for each fir's future prediction: full-, no- and partial-migration scenarios (Bateman et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Study area and species occurrence data

The MSWC extend from the western Himalayas and the Yarlung Zangbo Canyon to the Hengduan Mountains and the western Sichuan Plateau (Royden, Burchfiel, & van der Hilst, 2008; Zhao, 1990). Here, vast ridges and valleys spread from the Qinghai-Tibetan Plateau to the western rim of the Sichuan Basin with altitudes ranging from a few hundred metres to more than 7,000 metres (Royden et al., 2008). In the "three parallel river-running areas" (i.e. Lancangjiang, Nujiang and Jinshajiang Rivers), most of the mountain ridges are oriented generally in a north–south direction, for example Boxoilaling-Gaoligong Shan, Taniantawen Shan-Nu Shan and Mangkang Shan-YunLing (Royden et al., 2008). Their pronounced difference in elevation, heterogeneous geography and varied climate result in a high diversity of different vegetation types with high endemic species richness (~3,500 endemic vascular plant species) making the MSWC as one of the most important global hotspots of biodiversity (Li, 2018; Wu, 1980). For this study, the MSWC were identified as an area within the geographical coordinates of 20.6°–35.8°N and 85.4°–105.8°E (Figure 1).

Here, we summarized *Abies* according to the description of the Flora of China (Editorial Committee of Flora of China CAS, 1999; http://foc.iplant.cn/). There are 22 fir species in China, nine of which are both endemic and distributed in the MSWC (Table S1). However, some species do not have sufficient distribution data for successful modelling (Stockwell & Peterson, 2002). According to their current geographical distributions (Fan, 2006), six dominant and endemic fir species were selected and divided into three groups: "North"—*Abies recurvata* and *Abies faxoniana*, which mainly occur in the upper Minjiang River region; "Middle"—*Abies squamata* and *Abies ernestii*, which occur in the western Sichuan Plateau; and "South"—*Abies forrestii* and *Abies georgei*, which occur in the narrow Hengduan Mountains region (Figure 1; Figure 2; Table 1).

A total of 920 occurrences of the six fir species were obtained from the following four sources: (a) the Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/); (b) Global Biodiversity Information Facility (GBIF, http://www.gbif.org/); (c) field surveys (21 records);

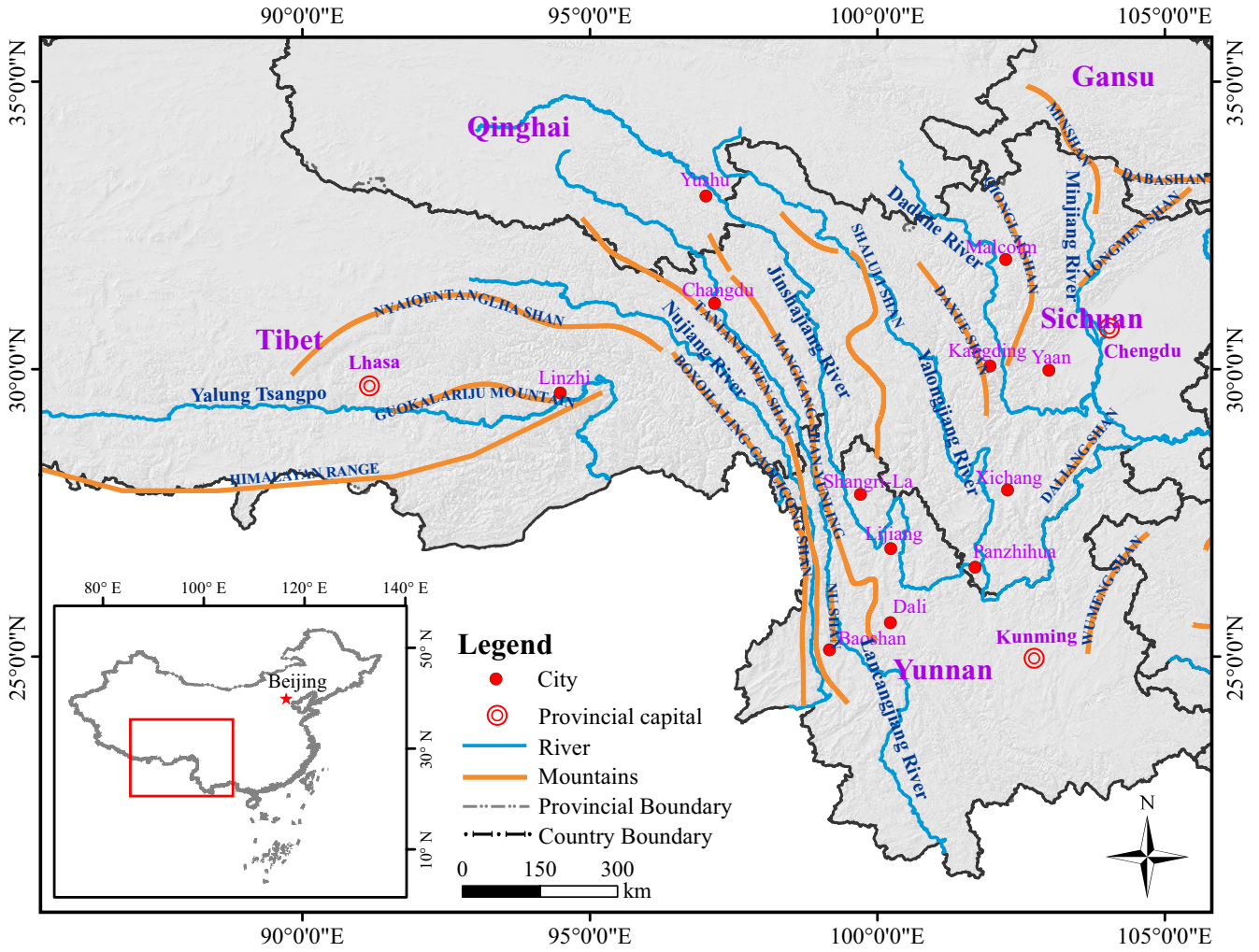


FIGURE 1 Geographical extent of the study area, spanning eastern Tibet, western Sichuan and northern Yunnan. The inset shows the study area (box in red) in relation to China. The locations of cities, rivers and mountains are provided for reference

and (d) published literature (see Table 1 and Appendix S1 in the supplemental files). Since some of these occurrences lacked geographical coordinates, Google Earth (http://ditu.google.cn/) served to complement the latitude and longitude information. Moreover, any species occurrences that were based on introduction and cultivation were excluded. Given that most SDM methods require input data to be spatially independent for the model to perform well (Naimi, Skidmore, Groen, & Hamm, 2011), SDMToolbox (Brown, 2014; http://sdmtoolbox.org/) was used to ensuring that only one occurrence record per species was used within each grid cell at a resolution of 30 arc-seconds (~ 1 km at the equator). Maps of the remaining species occurrences were then constructed using ArcGIS 10.3 (Esri, Redlands, CA, USA, http://www.esri.com) (Figure 2).

2.2 | Climatic variables and climate scenarios

We used an initial set of 22 climatic predictors, which included 19 bioclimatic variables (bio1 ~ 19), solar radiation (SR), wind speed (WS) and water vapour pressure (WVP) with 30 arc-second spatial resolution (~ 1 km at equator) obtained from WorldClim (http://www.worldclim.org/) (Fick & Hijmans, 2017; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (Table S2).

To avoid multicollinearity of variables (Graham, 2003), we examined the cross-correlation of the 22 variables using the "cor" function in R (R-Core-Team, 2015) and eliminated the highly correlated (|Pearson r| ≥ .8) climatic variables (Blach-Overgaard, Svenning, Dransfield, Greve, & Balslev, 2010). Because extreme temperature and humidity are often considered the most critical limiting factors affecting tree growth in alpine regions (Zimmermann et al., 2009), such variables were given priority in our study (see Table S5 for more details). Finally, out of the total 22 variables, only nine were selected as predictors, including BIO2 (mean diurnal range), BIO3 (isothermality), BIO4 (temperature seasonality), BIO5 (max temperature of warmest month), BIO11 (mean temperature of coldest quarter), BIO14 (precipitation of driest month), BIO15 [precipitation seasonality (coefficient of variation)], SR (solar radiation) and WS (wind speed) (Table S5).

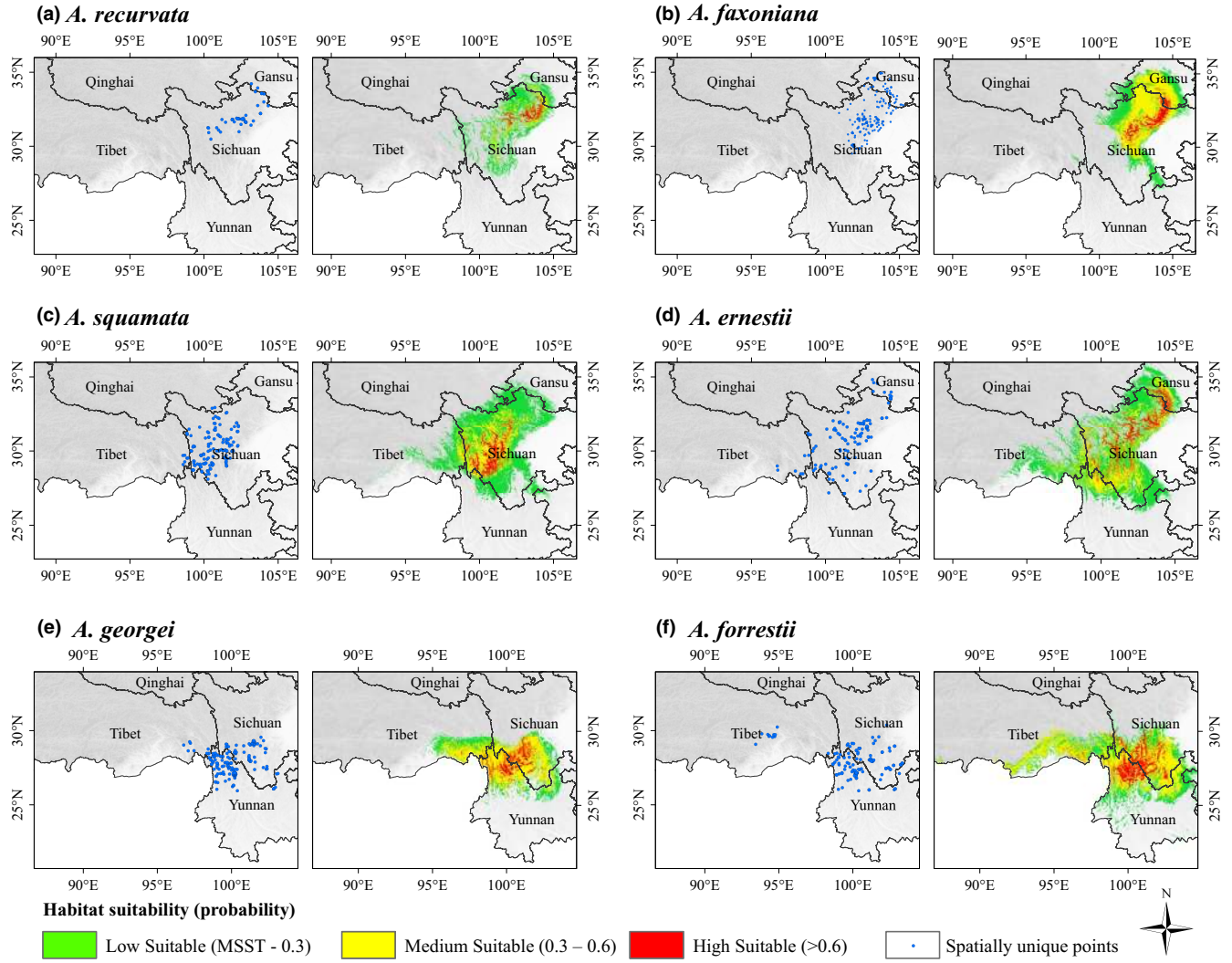


FIGURE 2 Occurrence records (left side of each secondary figure) and predicted distribution of current CSAs (right side of each secondary figure) for the six studied fir species

For global climate models (GCMs), we used BCC-CSM1-1 (Beijing Climate Centre, China Meteorological Administration), which is considered one of the more suitable GCMs for climate change research in China (Yang, Jiang, & Li, 2016). Two representative concentration pathways, RCP 4.5 (moderate emission scenario) and RCP 8.5 (pessimistic emission scenario), released by the IPCC Fifth Assessment Report (AR5) (IPCC, 2013; Meinshausen et al., 2011), were selected to represent the possible future climate scenarios. All future climatic layers were based on WorldClim v1.4 (Hijmans et al., 2005) at a 30 arc-second spatial resolution. For periods of 2041–2060 and 2061–2080 (Tables S3 and S4), the predictor layers were downloaded from WorldClim v1.4. Besides, we downloaded corresponding layers of the period 2021–2040 from CGIAR web portal (http://www.ccafs-climate.org) for the subsequent migration analysis. Like other studies (Chakraborty, Joshi, & Sachdeva, 2016; Zhang, Yao, Meng, & Tao, 2018), we assumed SR and WS to remain unchanged when projected into the future. Finally, all raster data were extracted to the regional extent of the study area with ArcGIS 10.3 (Esri).

2.3 | Evaluation of current and future habitat suitability

We used the Maximum Entropy approach (Maxent version 3.3.3 k; Phillips et al., 2006) to calibrate and to predict the CSAs of each species for the current period and projected CSAs for future periods (2040, 2060 and 2080) based on the nine selected climatic predictors. To reduce uncertainty caused by sampling artefacts, we randomly divided distribution data into training data (75%) and validation data (25%). To validate the robustness of the models, replications of 20 times were carried out using the subsampling method, in which the presence points are repeatedly split into random training and testing subsets, and the results were finally averaged. The maximum number of background points was set to 10,000, and the maximum iterations were set to 5000 times for seeking the optimal solution, while we used for the remaining parameters default values (Morales, Fernández, Baca-González, & Yoccoz, 2017; Radosavljevic & Anderson, 2014). The generated suitability maps

TABLE 1 Overview of distribution data and SDMs for each species investigated

Species	Number of records[a]	Final points used in SDMs[b]	MTSS[c]	Group
A. recurvata	51	44	0.074 (0.01)	North
A. faxoniana	250	199	0.106 (0.01)	North
A. squamata	164	138	0.065 (0.01)	Middle
A. ernestii	121	114	0.109 (0.02)	Middle
A. forrestii	139	124	0.130 (0.01)	South
A. georgei	195	165	0.137 (0.01)	South

[a]Number of each species' distribution data after correction.

[b]Number of spatially rarefied points at a resolution of 30 arc-seconds (~ 1 km at the equator).

[c]MTSS—maximum training sensitivity plus specificity. Threshold used for categorical classification; this threshold maximizes the cases where the model erroneously assigns unsuitable habitat (true negative) and misses suitable habitat (false positive). Values in parenthesis represent standard error.

were in ASCII format, so we converted them into a TIFF raster format using ArcMap 10.3 (Esri).

To convert the continuous suitability scores (range of 0 to 1) of the Maxent output into binary suitability, we used the maximum training sensitivity plus specificity (MTSS) threshold as recommended by Liu, Newell, and White (2016) for presence-only data like in our study. At the same time, we reclassified the suitability into four classes: unsuitable habitat (<MTSS), minimally suitable habitat (MTSS-0.3), moderately suitable habitat (0.3–0.6) and highly suitable habitat (>0.6). To explore the key climatic variables that shape the distribution of each species, we utilized a jackknife test with all model replications to rank the relative importance of the variables, and the response curves of each variable were visualized. To verify the accuracy of each model, we adopted the area under the curve (AUC) of the receiver operation curve (ROC), which was determined by the following criteria: poor (AUC < 0.8), good (AUC 0.90–0.95) and excellent (AUC > 0.95) (Guisan & Thuiller, 2005).

2.4 | Incorporating migration ability

To simulate the effects of migration ability on the accessibility of future suitable habitat areas, three different migration rates were assigned to all species: full migration (unlimited m/year), partial migration (200 m/year, Cheddadi et al., 2014; Xu, 1998; see Appendix S2 in the supplemental files for more details) and no migration (0 m/year). The full-migration (FM) scenario was obtained directly from the Maxent model default output applying the species-specific MTSS threshold, and it was the most optimistic assumption that species could colonize all suitable habitats under climate changes (Franklin, 2010). In contrast, the no-migration (NM) scenario was the most pessimistic scenario in that it assumed species could not migrate at all and only lose suitable areas as the climate changes. This scenario was achieved by restricting 2080 projections to the suitable pixels of the current predictive map (Franklin, 2010).

For the partial-migration (PM) scenario, we used the KISSMig model (Nobis & Normand, 2014), a simple 3 × 3 raster-based stochastic approach to simulate dynamic changes in species distributions on top of habitat suitability maps. We applied KISSMig simulations with suitability maps for the three consecutive periods of 20 years, that is 2021–2040, 2041–2060 and 2061–2080. As initial species distribution, we used the current Maxent prediction applying MTSS. In contrast to other publications using KISSMig with quantitative suitability values (Kissling, Blach-Overgaard, Zwaan, & Wagner, 2016; Nobis & Normand, 2014; Subba, Sen, Ravikanth, & Nobis, 2018), we used only suitability values 0 (unsuitable) and 1 (suitable) for migration simulation. Therefore, the simulated spread of the species into suitable areas was always at 200 m/year. Although in a previous KISSMig study alpha-shapes based on present species occurrences were used to restrict initial species distribution (Subba et al., 2018), we decided to use the entire suitable area, because otherwise, artificial edge effects biased the results and the predicted suitable area matched well with the species occurrences. The initial distributions of six species were assumed to be still valid in 2021. We presumed the migration rate, 200 m/year, remained unchanged, and for each period, the migration rate thus was 4 km/ 20 years or 12 km/ 60 years from 2021 to 2080.

2.5 | Quantify the magnitude and direction of range shifts

To quantify the magnitude of change in the projected distributions of each species across the two climate scenarios and the three migration scenarios, we compared the final distributions to the initial distributions and classified pixels as (a) expansion, (b) no change and (c) contraction. Then, we calculated the expanded, unchanged and contracted areas under all emission × migration scenarios in ArcMap 10.3 (Esri). Moreover, to verify hypothesis 3, we focused on providing a summary of the direction of range shifts of the six species. Given that the shapes of both the initial and projected species distributions were irregular, their boundaries cannot easily be determined. Many studies use, therefore, the shifts of centroids as a good measure of the direction of species' potential range change

(e.g. Thurm et al., 2018; Zhang et al., 2018). Here, we calculated the centroids for both current and future species distributions and used these centroids to project a vector arrow to indicate the magnitude and direction of range shifts using the SDMToolbox (Brown, 2014).

3 | RESULTS

3.1 | Important climatic factors and predicted current CSAs

The AUC values of all Maxent models were higher than 0.9 (Table S6 mean 0.988 ± 0.004), indicating that our SDMs had an excellent overall prediction ability. Among all variables, the three top-ranked factors were isothermality (BIO3), temperature seasonality (BIO4) and solar radiation (SR), whose cumulative relative importance to all species exceeded 65% (Table 2). The response curves of all variables can be found in the supplemental files (Figures S2 and S3). However, these three climatic variables varied considerably in their contribution rate among the species groups (Figure 3; Table 2). In particular, there was a remarkable difference in the contribution of BIO4 and SR between the "South" and "North" groups of species. Besides, for the "Middle" group of species, the three variables (BIO3, BIO4, and SR) had an almost equal contribution in shaping their distributions (Figure 3).

Overall, the species showed individualistic differences in their current CSAs (Figure 2). Among the six species, *A. recurvata* had the smallest CSAs (ca. 1.23×10^5 km^2) and its highly suitable areas were predicted primarily in Aba prefecture of Sichuan Province (Figure 2a; Table S7). Compared to the CSAs for *A. recurvata*, the current CSAs for *A. faxoniana* (ca. 2.11×10^5 km^2) were primarily located in Aba and Ganlan prefectures but were absent in the western Garzê prefecture of Sichuan Province. In addition, the CSAs of *A. faxoniana* also extended southward along the Minjiang River to northeastern Yunnan Province (Figure 2b; Table S7). By contrast, *A. squamata* (Figure 2c) and *A. ernestii* (Figure 2d) were estimated to have broader distributions that thoroughly covered the central MSWC (ca. 3.19×10^5 and 3.75×10^5 km^2, respectively). For the highly suitable areas, *A. squamata* was projected to occur primarily in the southern part of Garzê prefecture, while *A. ernestii* occurred not only in southern Garzê but also in eastern Aba and southern Ganlan prefectures (Figure 2c,d; Table S7). However, *A. forrestii* (Figure 2e) and *A. georgei* (Figure 2f) were largely confined to the southern MSWC (ca. 3.08×10^5 and 1.92×10^5 km^2, respectively). Furthermore, the junction of Sichuan, Yunnan and Tibet was the common highly suitable areas shared by the "South" group of species, and this region generally included Diqing, Lijiang, Xichang, Changdu and Linzhi prefectures (Figure 2e, f; Table S7).

3.2 | Projected future change in species distributions

Generally, our projections for 2080 based on the full-migration scenario indicated that all species differ in their CSAs changes among the RCP 4.5 and RCP 8.5, with some species dramatically expanding or contracting their CSAs. Under both RCP 4.5 and RCP 8.5 scenarios, by 2080, the CSAs of *A. recurvata* were predicted to expand in southern Gansu, western Sichuan and eastern Tibet and contract in the southern and eastern parts of its current range (Figure 4a). For *A. recurvata*, a sizeable net expansion in CSAs from the current period to 2080 was projected to occur in both emission scenarios, with a 50.1% expansion under the RCP 4.5 scenario and a 38.8% expansion under the RCP 8.5 scenario (Figure 5a; Table S8). In contrast, the projected CSAs of *A. faxoniana* underwent a less pronounced contraction, with a decline of 4.3% under the RCP 4.5 scenario and 3.7% under the RCP 8.5 scenario (Figures 4b and 5a; Table S8). The enormous inconsistencies in species' CSAs changes among the two emission scenarios occurred for *A. squamata* (Figure 4c). Under RCP 4.5, the projected CSAs of this species expanded in southern Gansu and contracted in the southern part of its current range. However, *A. squamata* was projected to expand in eastern Tibet and northern Yunnan and contract in the southern and northeastern parts of its current range under the RCP 8.5 scenario (Figure 4c). Notably, under the RCP 4.5 scenario, the CSAs of *A. squamata* were projected to contract by 12.9%, which was more than twice the 6.3% loss projected under the RCP 8.5 scenario (Figure 5a; Table S8). Under both emission scenarios, by 2080, the projections for *A. ernestii* revealed a pattern that its expanded CSAs were similar to that of *A. recurvata*, and its contracted CSAs was similar to that of *A. squamata* (Figure 4d). Regarding the changes in CSAs of *A. ernestii*, scenario RCP 8.5 showed a more pronounced contraction (17.4%) than that under scenario RCP 4.5 (1.8%) (Figure 5a; Table S8). *A. forrestii* (Figure 4e) and *A. georgei* (Figure 4f) were projected to expand their CSAs in western Sichuan and eastern Tibet, contract their CSAs in the southern part of their current ranges under the RCP 4.5 scenario, and further contract their CSAs in the eastern parts of their current ranges under the RCP 8.5 scenario. By 2080, both species showed expansions in their CSAs under the moderate scenario and contractions under the pessimistic scenario, with a 14.8% expansion for *A. forrestii* and a 22.2% expansion for *A. georgei* under the RCP 4.5 scenario and with a 1.7% contraction for *A. forrestii* and 39.0% contraction for *A. georgei* under the RCP 8.5 scenario (Figure 5a; Table S8). Simultaneously, we found that by 2080, currently highly suitable areas of most species will become less suitable regardless of the assigned scenario, especially for the "South" group of species (Figure 4; Table S7).

3.3 | Migration scenario analysis

The above changes in CSAs for all species under the two emission scenarios were produced under the unlimited or full-migration assumption. However, if these firs are completely unable to track changes in their CSAs, all species' distributions would be expected to decrease under both emissions scenarios according to our projections (Figure 4). In such a completely limited or no-migration scenario, under the RCP 4.5 scenario, the expected decreases in distributions for all species were 9.3% (*A. recurvata*), 12.0% (*A. faxoniana*), 15.9%

TABLE 2 Mean relative importance of each variable to the final SDM of each species studied

Species	BIO2	BIO3	BIO4	BIO5	BIO11	BIO14	BIO15	SR	WS
A. recurvata	**10.2**	**33.6**	2.2	6.7	6.8	0.2	0.6	**38.0**	1.8
A. faxoniana	0.6	**17.2**	**19.2**	0.6	3.3	10.4	9.0	**39.5**	0.3
A. squamata	2.3	**30.2**	**24.0**	2.7	5.8	5.7	1.7	**27.4**	0.3
A. ernestii	2.6	**19.4**	**22.9**	5.0	17.6	7.2	0.5	**23.4**	1.5
A. forrestii	0.1	**13.7**	**57.0**	5.7	**8.5**	7.3	1.5	5.1	1.0
A. georgei	1.1	**22.7**	**47.2**	10.5	1.8	0.9	0.9	**13.8**	1.0

Note: The variables highlighted in bold are the three top-ranked importance factors for each species. BIO2 = mean diurnal range (°C), BIO3 = isothermality (°C), BIO4 = temperature seasonality (°C), BIO5 = max temperature of warmest month (°C), BIO11 = mean temperature of coldest quarter (°C), BIO14 = precipitation of driest month (mm), BIO15 = precipitation seasonality (coefficient of variation) (%), SR = solar radiation (kJ m^{-2} day^{-1}) and WS = wind speed (m/s).

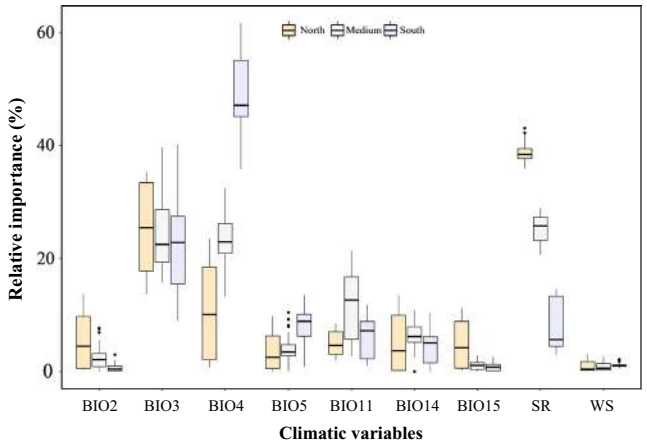


FIGURE 3 Boxplot (minimum, median, maximum, 25th and 75th percentiles) showing the distribution of the relative importance of the climatic variables used in Maxent within the three groups of species and for all model replications. Outliers are shown as black circles

(*A. forrestii*), 20.2% (*A. ernestii*), 20.4% (*A. georgei*) and 22.7% (*A. squamata*) (Figure 5c; Table S8). In addition, under the RCP 8.5 climate scenario, the corresponding decreases for all species were 11.2% (*A. faxoniana*), 19.1% (*A. squamata*), 19.9% (*A. recurvate*), 22.4% (*A. forrestii*), 30.6% (*A. ernestii*) and 46.9% (*A. georgei*) (Figure 5c; Table S8). In comparison to the no-migration scenario, the most significant change simulated in the partial-migration scenario occurred in *A. recurvata*, with an average 46.6% of newly colonized CSAs under RCP 4.5 and RCP 8.5 (Figure 5b; Table S8). At the same time, under the RCP 4.5 scenario, *A. georgei* expected to undergo an overall decrease (13.2%) in the partial-migration model rather than an increase (22.2%) in the full-migration model because approximately more than 80% of the colonizable CSAs were not accessible (Figure 5b; Table S8).

3.4 | Direction of future range shift

The vectors between the present and the future centroids indicated that the magnitudes and directions of the range shifts of all the species differed under both RCPs as well as the full- and partial-migration scenarios (Figure 6; Table S9; Figure S4 for full-migration result in the supplemental files). In the partial-migration scenario, all species differed in the directions of their centroids shifts from the current period to 2080 (Figure 6). *A. recurvata* was predicted to shift its distribution to the west (mean 7°) under both emission scenarios, while *A. faxoniana* was predicted to shift its distribution to the north (mean 295°). *A. ernestii* was predicted to shift its distribution to the north (5.1°) under the RCP 4.5 scenario and shift to the north-northeast (18.1°) under the RCP 8.5 scenario. In contrast, more complex shifts occurred in *A. squamata*, which was predicted to shift its distribution to the north-northeast (21.8°) under the RCP 4.5 climate scenario but shift to the west-northwest (273°) under the RCP 8.5 climate scenario. For *A. forrestii* and *A. georgei*, their distributions were expected to shift for each RCP very similarly towards higher latitude, but with different directions between the RCPs (Figure 6).

4 | DISCUSSION

4.1 | Key factors shaping species distributions

The importance of temperature-related variables and solar radiation on the current distributions of all fir species exceeded those of water-related variables (Table 2). The unique geography and weather conditions of the MSWC explained this discrepancy. The species we studied mainly inhabit the high mountain areas, where the annual precipitation is approximately > 900 mm due to the East Asian and southwestern monsoons, thus making it a humid region that enables these species to not experience drought stress (Farjon, 2001; Ye & Gao, 1979). The importance of the climatic key drivers, however, appears to be strongly correlated with the geographical location of each species (Figure 3). Generally, isothermality is regarded as the most decisive factor for firs in the MSWC (Chhetri et al., 2018; Liu et al., 2018). However, accounting for additional factors, apparent differences exist in the importance of solar radiation and temperature seasonality between our "North" and "South" species (Figure 3). Temperature-related variables, such as pre-growing season temperature (Guo et al., 2018), minimum air temperature (Li et al.,

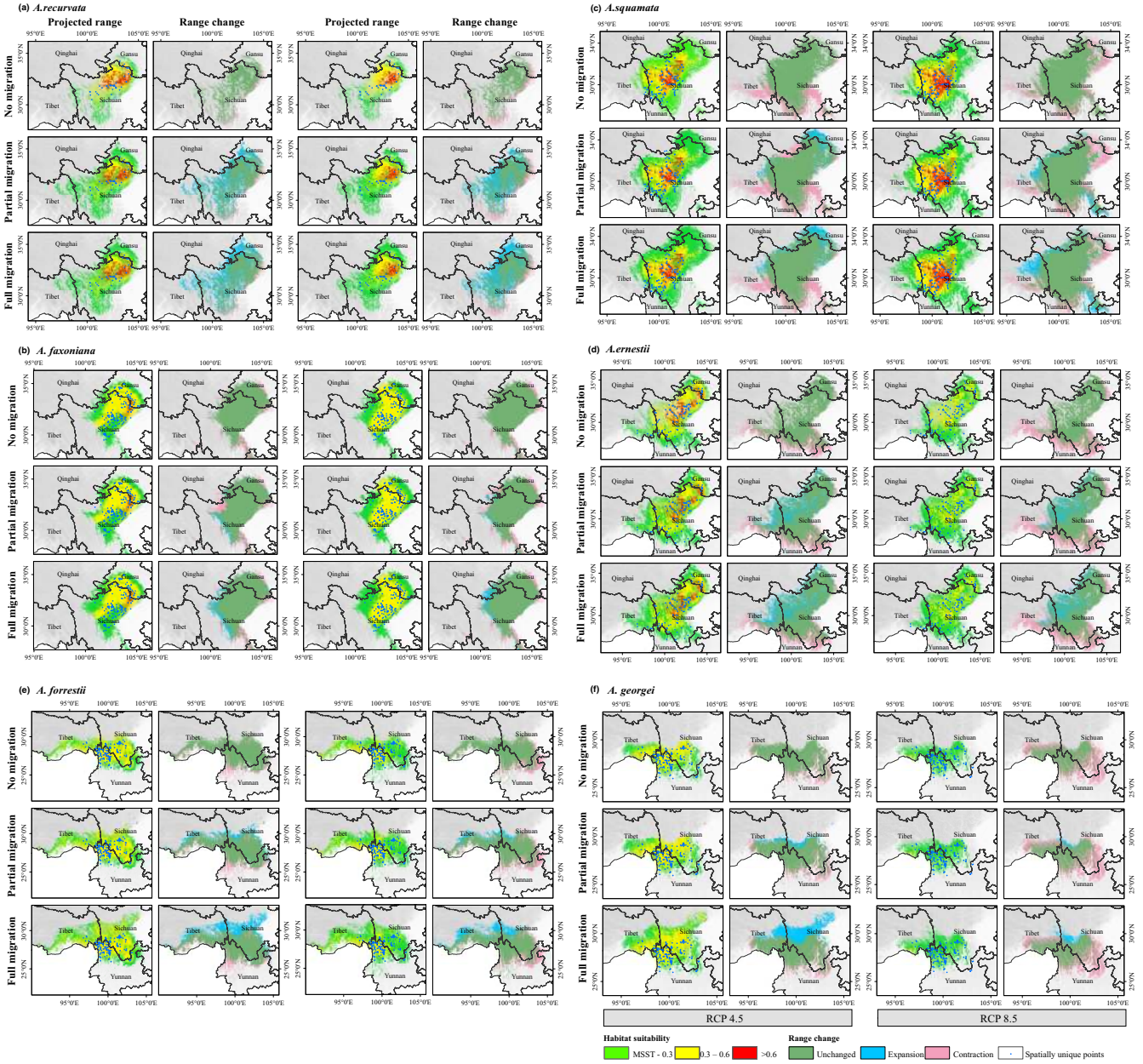


FIGURE 4 Projected future distributions of period 2060–2080 for the six studied fir species and the changes in areas between future and current distributions under two emission scenarios (RCP 4.5 and RCP 8.5) and three migration scenarios (full-, partial- and no-migration scenarios). a) *A. recurvata*, b) *A. faxoniana*, c) *A. squamata*, d) *A. ernestii*, e) *A. forrestii* and f) *A. georgei*

2017) and summer mean and minimum temperatures, have been reported as important factors for the growth and regeneration of fir species on the QTP (Yin et al., 2018), and further affect their large-scale distribution pattern (Benito-Garzón, Ruiz-Benito, & Zavala, 2013). On the other hand, solar radiation indirectly determines the precipitation and temperature patterns on the Earth's surface and regulates the composition, productivity and distribution of ecosystems through photosynthesis (Piedallu & Gégout, 2008). We emphasized the importance of solar radiation on the distribution of the "North" group of species which is consistent with findings of Zhang et al. (2016) and underline the necessity of incorporating solar radiation in species distribution modelling.

4.2 | Distribution dynamics under the full-migration scenario

In our first hypothesis, we stated that some fir species may benefit from future ACC and may have a broader potential distribution under the condition of unlimited migration. According to our full-migration assumption, this hypothesis was indeed confirmed; future climate change was suggested to be detrimental to the persistence of the current CSAs for most firs in the MSWC, but *A. recurvata* was expected to expand its CSAs by an average of 44.5% under both emissions scenarios (Figures 4a and 5a).

Compared with other full-migration projections, our optimistic forecast for *A. recurvata* was not consistent with the overall declining

trend of the genus *Abies* as highlighted by Liu et al. (2018) and Shao et al. (2017). Benefiting from future climate change, a large number of currently unoccupied areas in southern and western Sichuan will be potentially suitable for *A. recurvata* (Figure 4a). On the other hand, Liu et al. (2018) found at the genus level that the reduction in distribution area under the RCP 8.5 scenario was significantly higher than that under the RCP4.5 scenario. Although our projections for most species were consistent with this general finding, for *A. squamata*, the net loss of CSAs under the RCP 4.5 scenario was predicted to be twice as large as that under the RCP 8.5 scenario (Figure 5a). Obviously, the generalizations of these previous studies masked individual changes that were contrary to the overall trend, and our study identified such specific responses of fir species to climate change. Similarly, on the QTP, Chhetri et al. (2018) also predicted that the suitable area of *Abies spectabilis* would increase significantly in the future. At the same time, our full-migration scenario for *A. georgei* was more in line with that of Kou, Li, and Liu. (2011), and we both emphasized a less optimistic estimate of the future existence of this species under the more severe climate change scenario. However, *A. faxoniana* was the species least affected by ACC in our prediction; this projection was different from that of Kou et al. (2011), who predicted that its suitable areas would expand dramatically at the end of this century, even in southwestern Tibet. The prediction of Kou et al. (2011) was based on a fuzzy distribution data set and only three environmental variables. In comparison, the more accurate distribution data and comprehensive predictors used by our SDMs made our prediction of *A. faxoniana* (Figure 2b) closer to the actual distribution described by Fan (2006). Nevertheless, unlimited, long-distance migration seems unrealistic for mountain plants (Engler et al., 2009) except for the most vagile invasive species (Hellmann, Byers, Bierwagen, & Dukes, 2008).

4.3 | Migration constraints

Full-migration scenarios predicted potentially colonizable areas, which are inaccessible in the no-migration scenarios (Franklin, 2010). Similarly, under partial-migration scenarios, all the species studied were expected to decrease their suitable areas to a certain degree (Figure 5b). However, the partial-migration scenarios split all potentially colonizable areas into accessible and inaccessible areas. According to our results, the potentially colonized areas, especially for species of the "South" group, are significantly reduced in the partial-migration scenarios in comparison with the full-migration scenarios (Figure 5a,b). Obviously, this result reinforced our second hypothesis, and the most significant change occurred in *A. georgei* under the RCP 4.5 climate scenario, with more than 80% of its northern colonizable area is inaccessible in the partial-migration scenario (Figure 5b, Table S8). Our projections for *A. recurvata* suggested that its new future CSAs were mostly in the neighbourhood of its current CSAs and could be colonized relatively easily (Figure 4a). However, unlike *A. recurvata*, *A. georgei* and *A. forrestii* could not colonize much of their potential CSAs in the north, as they were too far from their current distributions (Figure 4e,f). The partial-migration assumption bridged the gap between the full- and no-migration scenarios and provided more realistic outcomes despite the simplicity of the migration assumptions.

Dynamic simulations using partial-migration scenarios are also able to detect potential changes in species ranges, which are not visible using static projections. *A. faxoniana* and *A. squamata*, for example, show under partial-migration and RCP 4.5 significant dieback regions at their northern distribution boundaries between Sichuan and Qinghai (Figure 4b,c). This range contraction is not detectable in the static no- and full-migration projections, because these regions are still climatically suitable in 2080. The simulated dieback occurs already until 2040 (Figure S5), and although both species start recolonizing parts of the dieback region afterwards, there is still a significant range contraction visible in 2080. Such simulated species dynamics and regional fluctuations of future climate are characterized by high uncertainties. Nevertheless, they help to identify potential risk areas of species range contractions under climate change, especially in times of increasing extreme events and forest diebacks (Anderegg, Kane, & Anderegg, 2013).

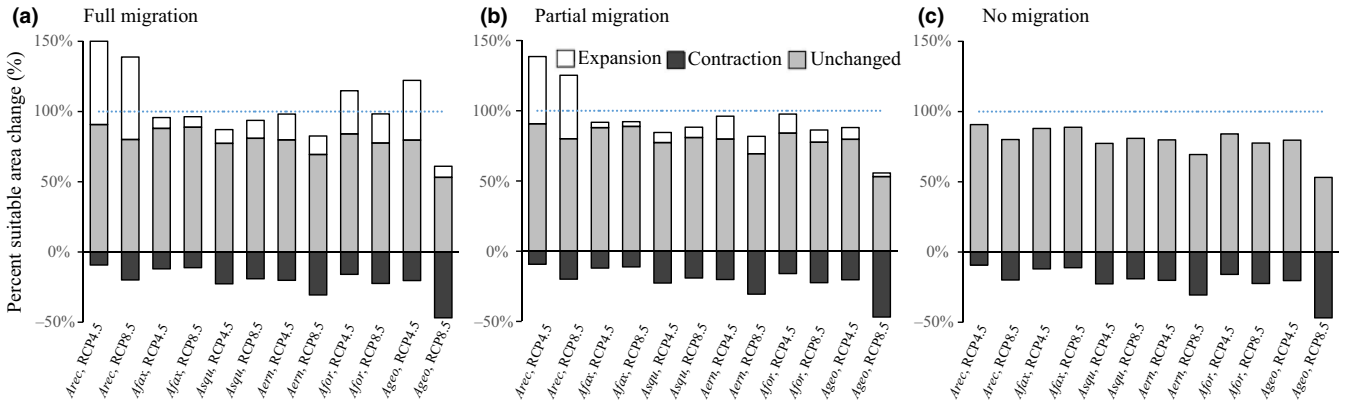


FIGURE 5 Percentage of the projected area in 2080 showing expansion, contraction or no change under RCP 4.5 and RCP 8.5. a) full-migration scenario, b) partial-migration scenario and c) no-migration scenario. Note that the dotted line in blue represents the current CSAs of each species (value = 100%). The distance between each column and this line represents the net rate of change in distribution areas

Another uncertainty concerns the migration abilities of species, which vary greatly among taxonomic groups (Bateman et al., 2013). McLachlan et al. (2005) found temperate broad-leaf species, such as the genus *Acer* and *Fagus*, migrate at approximately 172 m/yr and 214 m/yr, respectively, to track rapid ACC. Fitzpatrick et al. (2008) found that the simulated migration rate of c. 500 m/yr might be ideal for simulating the potential distribution of some broad-leaf species (*Banksia*) in Western Australia. In contrast, La Sorte and Jetz (2010) indicated a general statement that it was better to apply the no-migration scenario to future predictions of mountainous coniferous species. Based on a no-migration scenario, Dyderski et al. (2018) emphasized the threatened areas in the projections of *Abies alba*, rather than its large potential CSAs in Northern Europe, as the authors thought *A. alba* has a low migration ability. Reports of precise migration rates are, however, rare (Meier et al., 2012); therefore, it is difficult to determine which migration scenario is suitable for predicting the studied fir species. Interestingly, our study found a clear contrast in range shifts, especially in the "South" group of species when migration constraints were considered. Although the partial-migration rate utilized in this study may not accurately reflect the actual migration abilities of each fir species, the three migration scenarios together provided a more complete picture of the potential future changes in the distributions of the studied fir species.

4.4 | Direction of future range shifts

In this section, we discuss the third hypothesis that not all of the studied species consistently migrated northward, tracking future ACC. This hypothesis was supported by the results of the shifts in centroids of the distributions of all species. Generally, species migration direction seemed to be related to their location and emission scenarios. *A. recurvata* was expected to show a trend of westward migration under both climate change scenarios; *A. squamata*, *A. georgei* and *A. forrestii* were expected to migrate relatively uniformly westward under the RCP 8.5 scenario and northward under the RCP 4.5 scenario; and *A. faxoniana*, as well as *A. ernestii*, were expected to migrate northward under both climate change scenarios (Figure 6). Our projection on species westward migration was supported by Chhetri et al. (2018) and Dakhil et al. (2019) who both found that this westward trend exists in cold coniferous forest on the QTP. At the same time, Gao et al., (2016) used a dynamic global vegetation model to simulate the vegetation distribution on the

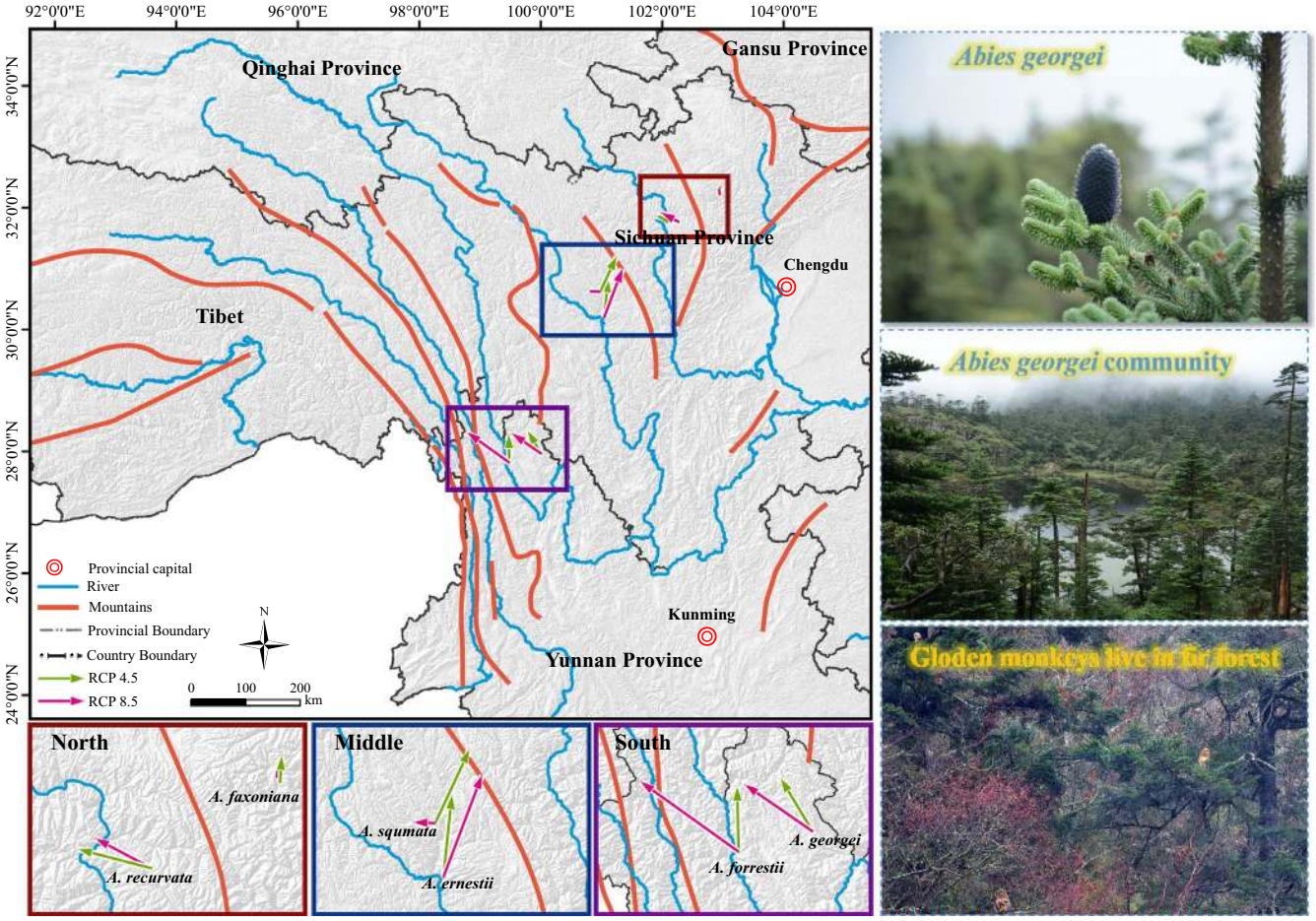


FIGURE 6 Shifts of centroids of projected distributions for each fir species under the partial-migration scenario. The pink arrows represent the RCP 8.5 emissions scenario, while the green arrows represent the RCP 4.5 emissions scenario

QTP and suggested that coniferous forests would gradually expand westward to replace herbaceous plants under the RCP 8.5 scenario by the end of this century. More importantly, the ancient fossils and pollen records located in strata of the Eocene and Oligocene in Lunpola Basin proved the historical prosperity of fir species in the hinterland of QTP (Xu, Tao, & Sun, 1973), which also reinforced our prediction. According to our projections, the studied firs will probably once again northward and westward migrate to the hinterland of QTP in response to future climate change.

Species responses to climate change vary with regions (Lindner et al., 2014). The direction in which species migrate with climate change depends on their specific physiological tolerance. Generally, species tend to migrate to higher latitudes, but there might be exceptions (Camille & Hanley, 2015). Shafer, Bartlein, and Thompson. (2001) suggested that as climate change occurs, the migration of some trees and shrubs in Western North America is not only northward but also in all directions, including southward, and affected by geographical constraints. In addition, Boisvert-Marsh, Périé, and Blois. (2016) found a gradual southward movement of *Abies balsamea* from 1970 to 2002 in North America because this species already occurred in high latitude regions with no possibilities to expand northward. Crimmins, Dobrowski, Greenberg, Abatzoglou, and Mynsberge. (2011) suggested that remarkable downhill shifts occurred in plants from the 1930s to the 2000s, tracking climate change in California. The individual differences in the migration of the studied species in the MSWC were not significant compared with the migration in these particular cases (Figure 6). However, analysing these subtle differences can support some assisted migration planning to mitigate the effects of future ACC on forests (Hällfors et al., 2016). This holds especially for species, such as, *A. forrestii* and *A. georgei* in our study, which very likely face difficulties tracking changes in their CSAs (Figure 4e,f; Figure 6).

4.5 | Risk to species in climate-sensitive areas

The junction of southern Sichuan and northern Yunnan was identified as a climate-sensitive area for species of the "Middle" and "South" groups, an area where firs were projected to lose much of their current CSAs (Figure S6). The alteration in temperature is a limiting factor for the growth of firs (Figures S1–S3). Besides, this region has a long history of intense human activities, especially near the city of Panzhihua, and the high level of industrial resource development makes its forests more vulnerable to human disturbance (Figure S7). More importantly, biogeographic barriers such as mountain ranges may limit the migration of these species (Wason, Bevilacqua, & Dovciak, 2017). Unfortunately, as these fir species of "South" group have reached almost the maximum height of the mountains, there may be limited opportunity to escape global warming through changes in elevation (Table S1, Fan, 2006). Hence, long-distance migration is the only option. We speculate that the barriers of mountains and rivers in the "three parallel river-running areas" could prevent a large number of seeds from reaching suitable habitats in time as the climate changes, resulting in an expansion rate failing to catch up with habitat loss.

5 | CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

Our climate niche models identified solar radiation as a key factor shaping the distribution of the "North" group of species, while temperature seasonality was identified as a key factor affecting the "South" group of species. We found that species in the southern part of the MSWC seemed to be more threatened by climate change, and this threat was amplified after limited migration was added as well as under the severe climate change scenario. Consequently, these species may face a higher risk of severe habitat loss in the future; hence, conservation assessment and planning are urgent priorities for these species that are endemic, dominant and considered keystone species of the fir forests in Southwest China. Although the projections of species distributions were developed under unavoidable simplified assumptions and uncertainties, they indicate potential challenges for *Abies* conservation and underscore the importance of incorporating migration ability into climate change effect assessments.

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CONFLICT OF INTEREST

None of the authors has any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The used online database of all species distribution data and environmental layers have been cited in the manuscript and indicated with accessible URL. The modelling data of this study are publicly available via GitHub (https://github.com/optiforziyan/Liao-et-al-2019).

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BIOSKETCH

Ziyan Liao research focuses on biogeography and macroecology, ecological methodologies and modelling, species diversity, biological conservation and spatial statistics. His current research involves simulating the distribution dynamics of woody plants in China but also including analyses from landscape scales to global.

Author Contributions: Z.L., L.Z. and K.P. conceived the idea and designed the simulations; X.W. collected the data; K.W., M.A.D. and X.T. presented the method and analysed the data; M.D., Q.X. and B.P. improved the manuscript; M.P.N. contributed new methods to revisions of the manuscript. All authors discussed the results and reviewed the manuscript.

SUPPORTING INFORMATION

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

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