DISTRIBUTIONAL RANGE SHIFTS IN RESPONSE TO CLIMATE CHANGE: A CASE STUDY OF CONIFER SPECIES ENDEMIC TO SOUTHWESTERN CHINA

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(Received 14th Aug 2022; accepted 11th Nov 2022)

Abstract. Climate change is widely expected to influence geographic distribution and range shifts of plant species. Southwestern China, which has been identified as one of the global biodiversity hotspots, is experiencing a warming trend that is well above the global average. *Pinus yunnanensis* is a mountainous conifer species endemic to southwestern China. However, little is known about its specific responses to future climate change. Here, based on a maximum entropy (MaxEnt) model, we integrated environmental factors, bioclimatic variables, and species occurrence data from extensive field surveys to project the potential suitable habitats of *P. yunnanensis* for the years 2050 and 2090 under two climate scenarios. According to our projections, *P. yunnanensis* generally experienced a suitable habitat loss in the coming decades, and there was a clear acceleration of habitat loss with the severity of climate scenarios. Moreover, the suitable habitat of *P. yunnanensis* showed a slight southward and downslope shift in response to climate change. Our results indicated that temperature-related factors and solar radiation, especially temperature seasonality, lowest temperature in the coldest month, and mean diurnal range, performed better than precipitation and topo-soil factors in explaining species distributional dynamics. In addition, we identified southern Sichuan and north-central Yunnan as long-term refuges for *P. yunnanensis* under future climate change, while southeastern Tibet should be protected as a priority conservation area. Our results can be used to guide long-term dynamic monitoring and provide a basis for conservation management of this endemic species.

Keywords: *coniferous forests, climate change, species distribution, conservation priority, mountain ecosystems*

Introduction

Climate is known as a key driver of the physiological processes associated with species survival (Dyderski et al., 2017). Its change poses a serious threat to biodiversity hotspots (Casazza et al., 2021; Manes et al., 2021). Rising temperatures in these regions obviously affect the distribution of plant species, especially those that are geographically restricted, such as endemic species (Hadjou Belaid et al., 2018). The geographical distribution patterns of species are widely based on their specific physiological tolerances to various environmental factors (Pecl et al., 2017; Williams and Blois, 2018) such as temperature, precipitation, sunshine duration, soil, and terrain (Huo and Sun, 2021). When climate-induced changes exceed their tolerance thresholds, species either adapt in situ to the new environment or shift their distributional range to track more suitable habitats (Pecl et al., 2017; Williams and Blois, 2018; McHenry et al., 2019). Climate warming accelerates changes in natural ecosystems, leading to irreversible habitat fragmentation and loss (Zhang et al., 2021). Plant species are probably unable to adapt to rapid climate change through evolution in a short period

(Liao et al., 2019), consequently facing a “nowhere-to-go” situation (Hülber et al., 2016). According to existing projections, one sixth of the species on Earth and 84% of mountain endemic species will be at high risk of extinction if climate change proceeds as expected (Urban, 2015; Manes et al., 2021).

Shifts in distributional range are the result of species tracking the movement of their favorable climatic conditions. In general, the geographical distribution of species shifts towards higher latitudes and elevations to cope with contemporary climate change (Freeman et al., 2018; He et al., 2019; van Beest et al., 2021), reflecting the impact of temperature gradients on species distributions (Fei et al., 2017; Williams and Blois, 2018). For example, species ranges have been proven to shift poleward at a rate of more than 16 km per decade in the Northern Hemisphere and upward at a rate of 11 m per decade in mountain ecosystems (Chen et al., 2011). Nevertheless, a few cases of movement towards longitudinally or lower altitudes have also been observed (Lenoir and Svenning, 2014; Fei et al., 2017; Liang et al., 2018). In addition, studies have also found that some high-elevation species can stay in place longer, they do not need to move as far to track suitable climatic conditions as they have broader thermal tolerances (Mamantov et al., 2021). These findings indicate that shifts in species range tend to be multidirectional (Fei et al., 2017; Williams and Blois, 2018) and that their responses to climate change are divergent (McHenry et al., 2019) and more complex than expected (Liang et al., 2018).

Although climate-only model has been extensively applied to predict species distribution, it overemphasized the importance of hydrothermal conditions. Unidirectional changes in species distribution driven by temperature, such as shifts along an altitude gradient, may underestimate the actual impact of climate change (Lenoir and Svenning, 2014), thereby masking climate vulnerability of species and causing a biased assessment (McHenry et al., 2019; Ma et al., 2021). Given that the potential impacts of variables other than temperature and precipitation on species range shifts are apparent (Fei et al., 2017; Williams and Blois, 2018), a combination of climate and other non-climatic factors should be considered in multifactorial models (e.g., accounting for soil and topo-hydrological factors or a broader set of environmental variables). This can improve model performance and accuracy (McHenry et al., 2019), as well as reinforce the importance of non-climatic variables in understanding the response of species to climate change (Zhong et al., 2021).

Unprecedented global warming over the past few decades is undoubtedly reshaping distribution pattern of species (Pecl et al., 2017), particularly in mountainous areas (Dagnino et al., 2020), which typically harbor a high proportion of endemic plants (Giménez-Benavides et al., 2018) and the greatest biodiversity on Earth (Mamantov et al., 2021). Additionally, mountainous areas are ideal places for evaluating the ecological impacts of climate change (Giménez-Benavides et al., 2018) and priority areas for conservation management (Manes et al., 2021). Species occurring here are more vulnerable to temperature rise (Freeman et al., 2018; He et al., 2019) and therefore deserve special attentions because of their specific habitats (Dagnino et al., 2020) and relatively weak migration capacity (Hadjou Belaid et al., 2018). However, the influences of climate change on mountain endemic species remain poorly understood (Dagnino et al., 2020). Therefore, it is more urgent than ever to understand the underlying mechanisms of how species’ range shifts in response to rapid climate change (Santini et al., 2021), especially the analyses of species-specific range dynamics

(Fadrique et al., 2018). This is of great significance for developing scientific and effective conservation strategies for species persistence in ecologically important area.

Species distribution models (SDMs), which integrate species occurrence data with environmental variables and global climate models (GCMs), have long been the effective method to evaluate species range shifts and their drivers (Casazza et al., 2021) for most biological groups (Hülber et al., 2016). *P. yunnanensis*, is a representative temperate coniferous species endemic to southwestern China. It occurs at mid-elevation areas, and plays a vital ecological role in climate regulation, nutrient cycle, carbon sequestration, soil conservation and biodiversity maintenance. *P. yunnanensis* is vulnerable to climate warming under harsh conditions (Shen et al., 2020), thus deserves special attention in biological conservation against climate change. Here, we used SDM to predict potential habitat of *P. yunnanensis* in southwestern China based on an extensive investigation and associated environmental variables. The objectives of this study were to identify the main factors influencing potential distribution of *P. yunnanensis*, and further explore its range shifts in projected distributions from current to future periods under different climate scenarios.

Materials and methods

Study area

The study area covers an enormous part of southwestern China, which lies between 78.39° to 109.55° E and 21.15° to 36.48° N, including Yunnan, Sichuan, Guizhou provinces, and Tibet Autonomous Region (*Fig. 1*). It covers almost 27.96×10^5 km^2 with an elevation range from 98 m to 7674 m. This region is one of the most important global biodiversity hotspots identified by Conservation International, is experiencing an unprecedented warming trend that is much higher than the global average (Liao et al., 2019). Moreover, this region is characterized by an extremely complex terrain, which are dissected by deep gorges through the main Asian rivers (Huo and Sun, 2021). Heterogeneous topography and various climate result in a remarkably high diversity and a mass of endemic species. Many species were confined to mountainous areas of this region, such as the Hengduan Mountains and the Ailao Mountains (Li et al., 2021).

Species occurrence data

The occurrence data of *P. yunnanensis* were collected from extensive field surveys conducted in 2019. The geographical coordinates of *P. yunnanensis* were recorded only when it appeared as a dominant species or a constructive species. To eliminate potential spatial autocorrelation or sampling bias, a spatial thinning method was applied to the study. We created a grid of 5 km × 5 km using ArcGIS10.2 (Eris, USA) and randomly selected one occurrence record from each grid cell. Finally, a total of 2530 available occurrence points of *P. yunnanensis* served as presence-only data and were used to build species distribution model.

Environmental data and processing

We initially collected a set of 27 environmental variables pertaining to climate, terrain, and soil for modeling the distribution of suitable habitat for *P. yunnanensis* in this study.

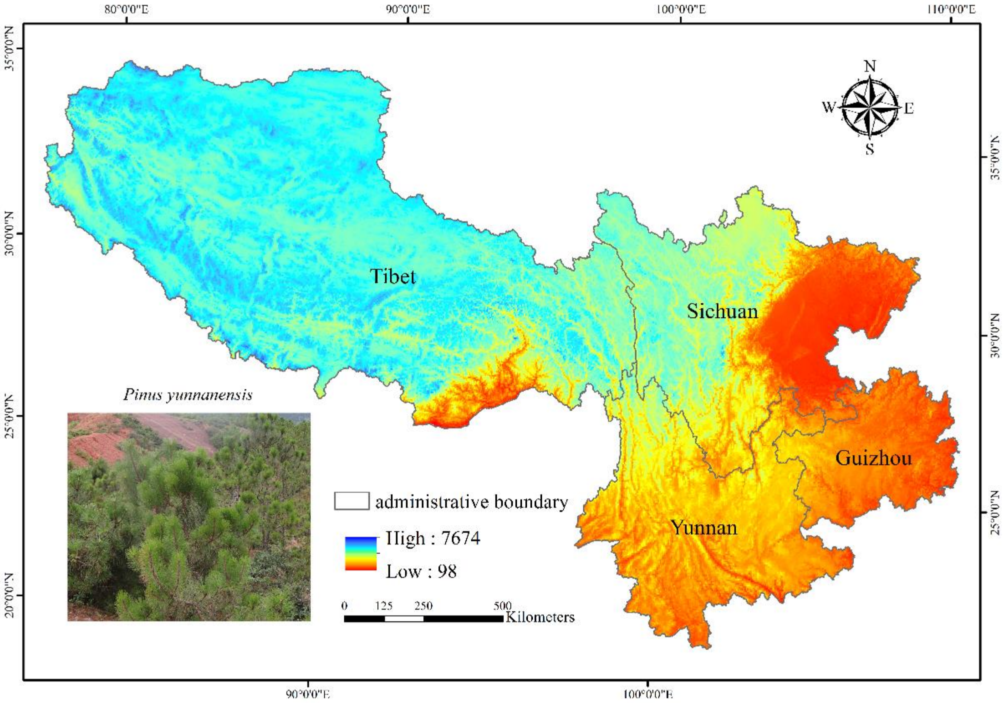


Figure 1. Location of the study area

Nineteen bioclimatic variables (bio1−bio19) include the annual mean temperature, temperature seasonality, annual precipitation, etc. for current climatic conditions (averaged across 1970−2000) and two future climate change periods, i.e., 2050s (2041−2060) and 2090s (2081−2100), were freely derived from WorldClim datasets ver. 2.1 (https://www.worldclim.org/), with a spatial resolution of 2.5 arcminutes. These bioclimatic variables, which represent annual trends, seasonality, and extreme environmental factors (Shishir et al., 2020), are considered important drivers of species distributions and are widely used in species distribution modeling (Román-Palacios and Wiens, 2020).

Additionally, the BCC-CSM2-MR global climate model developed by the National Climate Center (Beijing, China) was used to simulate future climate change scenarios. It was considered suitable for climate change research in China. In this study, bioclimatic data corresponding to two shared socioeconomic pathways (SSPs), namely SSP245 and SSP585 from the Coupled Model Inter-comparison Project Phase 6 (CMIP6) were considered to represent the possible climate change scenarios in the future. SSP245 and SSP585 represent medium and high emission forcing scenarios, with radiative forcing of 4.5 W/m^2 (~540 ppm CO_2) and 8.5 W/m^2 (~940 ppm CO_2) by 2100, respectively (Xu et al., 2022).

Topographic data (i.e., elevation and aspect) were extracted from the Digital Elevation Model (DEM) with a 90 m spatial resolution. DEM was downloaded from the geospatial data cloud (http://www.gscloud.cn/). In addition, edaphic variables at a scale of 1:1000000 comprising soil texture and classification, were obtained from the Resource and Environment Data Cloud Platform (http://www.resdc.cn/). Topographic and edaphic data are assumed to be constant in both current and future modeling (Liang et al., 2021). All the environmental variables were resampled to same resolution (Zhong et al., 2021) in the ArcGIS 10.2.

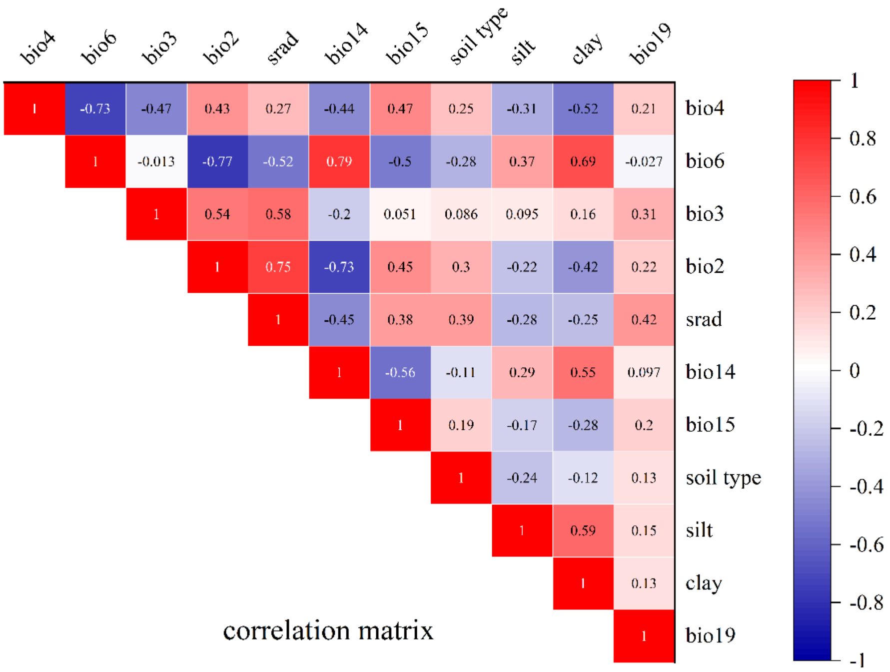
To avoid model overfitting caused by multicollinearity, a correlation matrix between each pair of the environmental variables was performed. Variables with low correlation coefficient ($|r| < 0.80$) were retained while those with high correlation coefficient ($|r| \geq 0.80$) and less ecological importance for the species were eliminated from model building (Brandt et al., 2017). Finally, seven bioclimatic variables including mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), min temperature of coldest month (bio6), precipitation of driest month (bio14), precipitation seasonality (bio15) and precipitation of coldest quarter (bio19), along with other three edaphic variables (clay percentage, silt percentage and soil type) and solar radiation were selected for model input (*Table 1; Fig. 2*).

Table 1. *Bioclimatic and other environmental variables used for model input*

Type	Variables description	Code	Unit
Bioclimate	Mean diurnal range	bio2	°C
	Isothermality	bio3	−
	Temperature seasonality	bio4	−
	Min temperature of coldest month	bio6	°C
	Precipitation of driest month	bio14	mm
	Precipitation seasonality	bio15	−
Soil	Precipitation of coldest quarter	bio19	mm
	Soil type	−	Categorical
Solar radiation	Clay percentage	−	%
	Silt percentage	−	%
	Solar radiation	srad	kJ·m^{-2} day^{-1}

Species distribution model

The maximum entropy (MaxEnt) model (version 3.4.1), a machine learning algorithm that maps habitat suitability with presence-only records (Phillips et al., 2006), was employed as the preferred approach to project the potential distribution based on the geo-referenced occurrence data of target species and selected variables. It is a widely used tool for environmental niche modeling and species distribution because of its great performance in different spatial modeling (Gomes et al., 2020). Randomly 75% of the occurrence records were assigned for model training, while the remaining 25% were used for testing. To ensure the model has adequate time to converge, the maximum iterations were set to 5000 (Rana et al., 2021; Zhong et al., 2021). Other parameters in the model were set as default. The model performance was evaluated by the area under the receiver operating characteristic (ROC) curve (AUC) because of its independence from threshold selection (Fois et al., 2018). In general, AUC ranges from 0.5 to 1.0, with values > 0.8 indicating that the prediction accuracy of the model is good (Phillips et al., 2006). More robust results were evaluated based on the average output of ten replicates. In addition, a jackknife test was performed to assess the permutation importance of each variable in datasets (Phillips et al., 2006); variables with a permutation importance value greater than 5% serving as the main environmental factors influencing distribution of *P. yunnanensis*.



	bio4	bio6	bio3	bio2	srad	bio14	bio15	soil type	silt	clay	bio19
bio4	1	-0.73	-0.47	0.43	0.27	-0.44	0.47	0.25	-0.31	-0.52	0.21
bio6		1	-0.013	-0.77	-0.52	0.79	-0.5	-0.28	0.37	0.69	-0.027
bio3			1	0.54	0.58	-0.2	0.051	0.086	0.095	0.16	0.31
bio2				1	0.75	-0.73	0.45	0.3	-0.22	-0.42	0.22
srad					1	-0.45	0.38	0.39	-0.28	-0.25	0.42
bio14						1	-0.56	-0.11	0.29	0.55	0.097
bio15							1	0.19	-0.17	-0.28	0.2
soil type								1	-0.24	-0.12	0.13
silt									1	0.59	0.15
clay										1	0.13
bio19											1

Figure 2. *Correlation matrix of variables selected for Maxent model*

Additionally, potential habitat suitability generated in this study was reclassified into four types: unsuitable (<0.1), low suitability (0.1–0.3), medium suitability (0.3–0.6), and high suitability (>0.6). Areas and centroids of suitable habitats were calculated in ArcMap 10.2 for each period and climate scenario to estimate the potential range shifts (McHenry et al., 2019; Naudiyal et al., 2021).

Results

Model performance and importance of variables

Model performance for predicting the potential distribution of *P. yunnanensis* was good, with a mean AUC value of 0.863 ± 0.001 for the current projection. According to the results of jackknife test (*Fig. 3*), temperature-related factors (i.e., bio4, bio6 and bio2) showed a greater importance in driving the potential distribution of *P. yunnanensis*, with the greatest influence of the temperature seasonality (bio4, 50.89%), followed by the min temperature of coldest month (bio6, 29.84%), the mean diurnal range (bio2, 7.30%) and solar radiation (srad, 6.0%), accounting for a cumulative contribution of more than 90%. In comparison, precipitation-related factors (i.e., bio14, bio15 and bio19) and edaphic variables had less importance. Overall, bioclimatic variables are more important than non-climatic variables in the distribution of *P. yunnanensis*.

Response curves of the main environmental factors under current climatic conditions showed unimodal effects on the potential distribution (*Fig. 4*), indicating that the suitable habitats (existence probability > 0.5) for the occurrence of *P.*

DOI: http://dx.doi.org/10.15666/aeer/2101_041058

yunnanensis were 380−550 for temperature seasonality (bio4), −7.5−6 °C for min temperature of coldest month (bio6), 8.5−12 °C for mean diurnal range (bio2), and 1.58×10^5−1.89×10^5 kJ·m^{-2}·day^{-1} for solar radiation (srad).

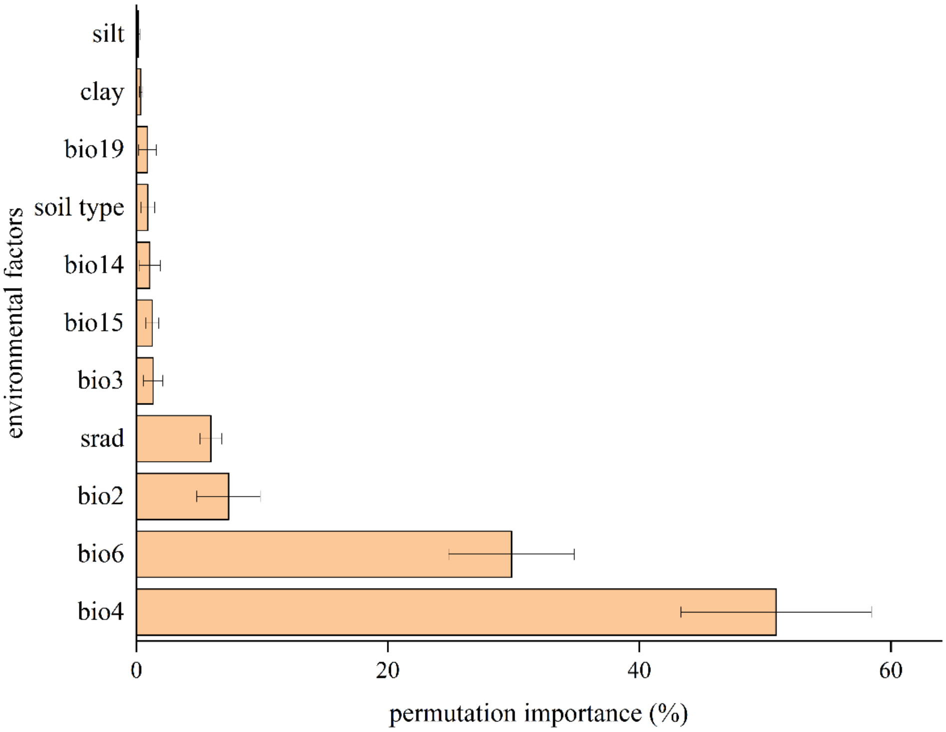


Figure 3. *Permutation importance of selected environmental factors based on the jackknife test*

Potential distribution under current and future climate scenarios

Potential distribution of *P. yunnanensis* in response to the current and future climate scenarios for 2050s and 2090s, obtained by Maxent model are shown in *Figure 5* and *Table 2*. Model projections showed that current total area of suitable habitat was expected to be 68.51×10^4 km^2, with the most suitable habitat was mainly concentrated in southern Sichuan and most areas of Yunnan except southern parts, covering an area of about 30.22×10^4 km^2 (*Fig. 5a; Table 2*). However, high-suitability habitat decreased to 29.37×10^4 km^2 under SSP245 and to 28.95×10^4 km^2 under SSP585 by the 2090s, with a reduction of 2.80% and 4.22% compared to the current, respectively (*Figs. 5d, e; Table 2*). While for the medium- and low-suitability habitats, they scattered in western and southern Yunnan, western Guizhou, central Sichuan, and extend westward to southeastern Tibet, occupying 24.58×10^4 km^2 and 13.71×10^4 km^2, respectively (*Fig. 5a; Table 2*). By the 2090s, medium-suitability habitat decreased to 23.28×10^4 km^2 under SSP245 and to 22.20×10^4 km^2 under SSP585 with a reduction of 5.29% and 9.68% compared to the current, respectively; low-suitability habitat increased to 16.47×10^4 km^2 and 16.88×10^4 km^2, with an increase of 20.13% and 23.12% compared to the current, respectively (*Table 2*). Overall, habitat suitability was not evenly distributed throughout the whole area. In addition, the conversion area of low suitability habitat to non-suitable habitat under SSP245 and SSP585 were 1.67×10^4 km^2 and 2.30×10^4 km^2 by the 2090s, respectively.

The projected range of *P. yunnanensis* varied across different periods and future climate scenarios. Changes in amount of suitable habitat were shown in *Figure 6* and *Table 2*. Total suitable habitat was projected to undergo a trend of contraction in most climate change scenarios and periods. Under the SSP245 scenario, suitable habitat shifted from a decrease in the 2050s to an increase in the 2090s. In the 2050s and the 2090s, the net increase in suitable habitat decreased obviously with increasing radiative forcing (from SSP245 scenario to SSP585 scenario) (*Fig. 6*). The gains and losses of distribution ranges were mainly along the boundaries of the current distribution under the future climate scenarios. The potential losses of the habitats are mostly located in central and western Sichuan and southeastern Tibet, which corresponded to the southeastern edge of the Qinghai-Tibet Plateau. In contrast, the habitat gains mainly occurred in southern Yunnan and parts of northern Sichuan (*Fig. 6*). The increase of suitable areas in western Guizhou and southern Yunnan was more pronounced under SSP245 than under SSP585, both by the 2050s and by the 2090s (*Fig. 6*).

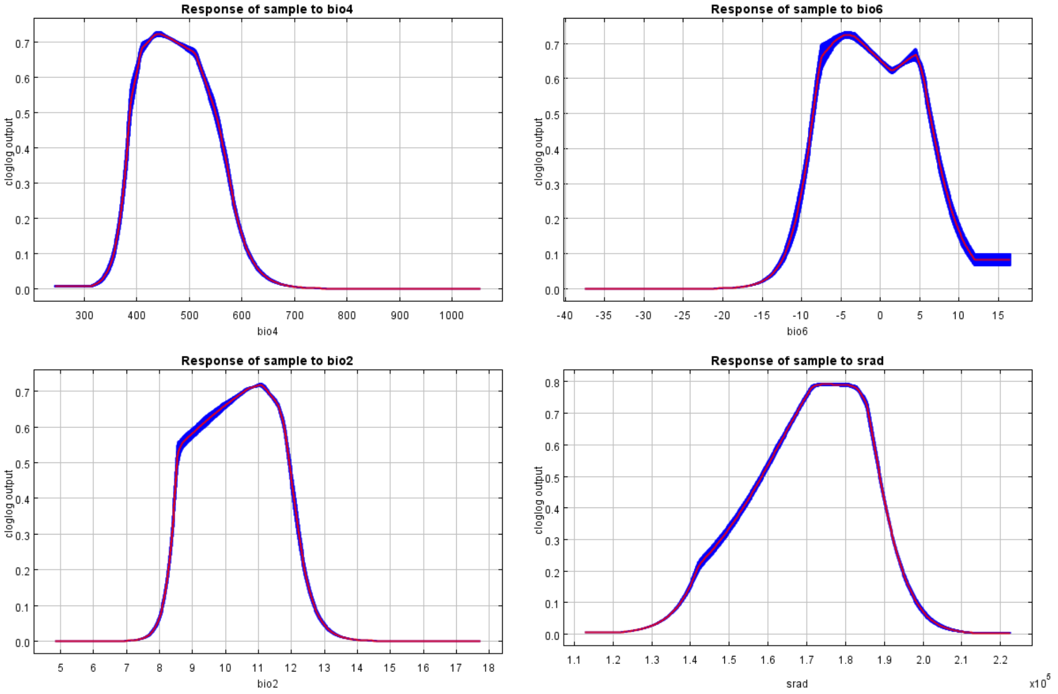


Figure 4. *Response curves of the main environmental factors on species distribution. Red curves show the mean value and blue margins are ± SD calculated by 10 replicates*

Table 2. *Suitable distributional areas of P. yunnanensis under different climate scenarios in different periods (10^4 km^2)*

Suitability class	**Current**	**SSP245**		**SSP585**	
		2050s	**2090s**	**2050s**	**2090s**
Low	13.71	15.64	16.47	14.74	16.88
Medium	24.58	22.26	23.28	22.76	22.20
High	30.22	27.78	29.37	29.92	28.95
Total suitability	68.51	65.68	69.12	67.42	68.03

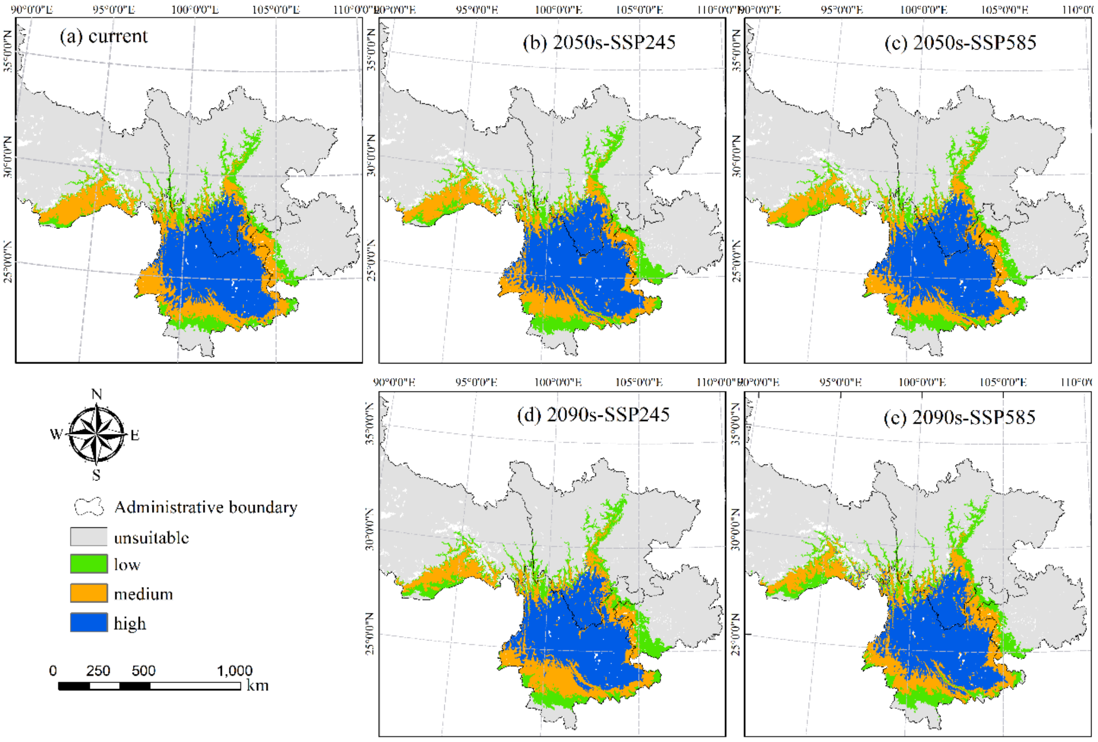


Figure 5. *Distributional range shifts of P. yunnanensis in southwestern China under different climate change scenarios and periods*

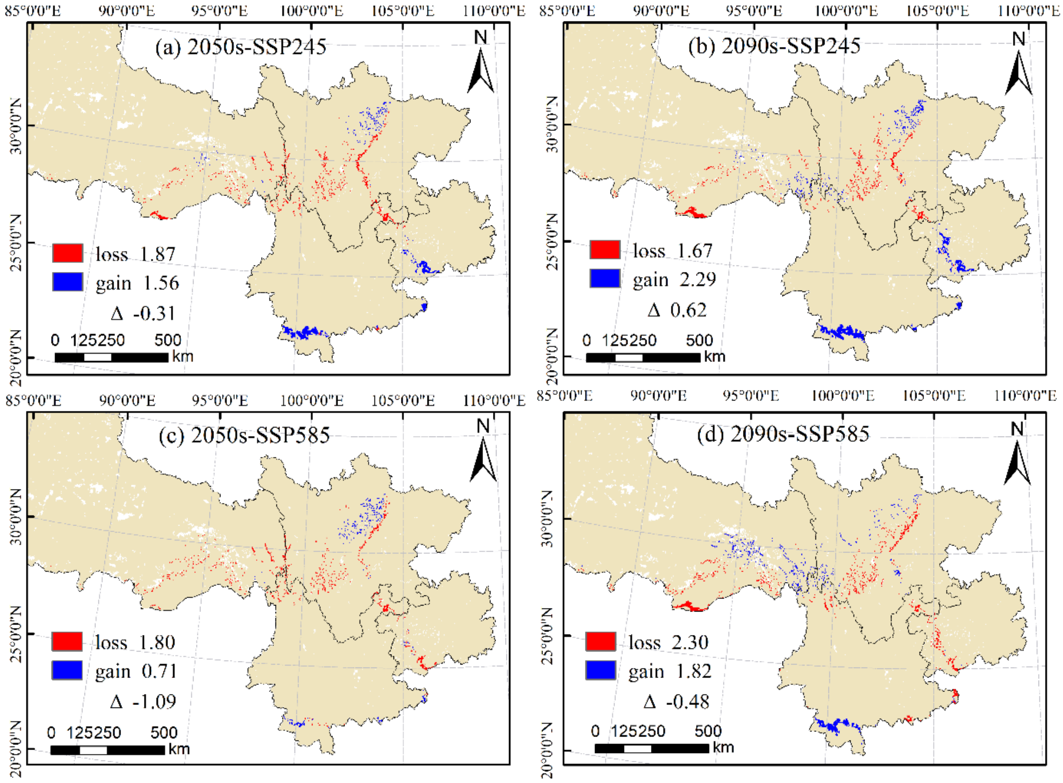


Figure 6. *Predicted range changes of P. yunnanensis by the 2050s and 2090s for SSP245 and SSP585 scenarios compared with the current condition (10^4 km^2)*

DOI: http://dx.doi.org/10.15666/aeer/2101_041058

Suitable habitat shifts

Shifts in distributional range were further estimated by the centroids of each suitable habitat for different climate scenarios. The distribution centroids of *P. yunnanensis* under current and future climate scenarios are all located in northwestern Yunnan. Suitable habitat of *P. yunnanensis* was predicted to migrate to lower latitudes, implying a southward shift in their distribution range under future scenarios (*Fig. 7*). In addition, its suitable habitat also exhibited altitudinal migrations, with a slight decrease in elevation under most of future climate scenarios (*Fig. 7*).

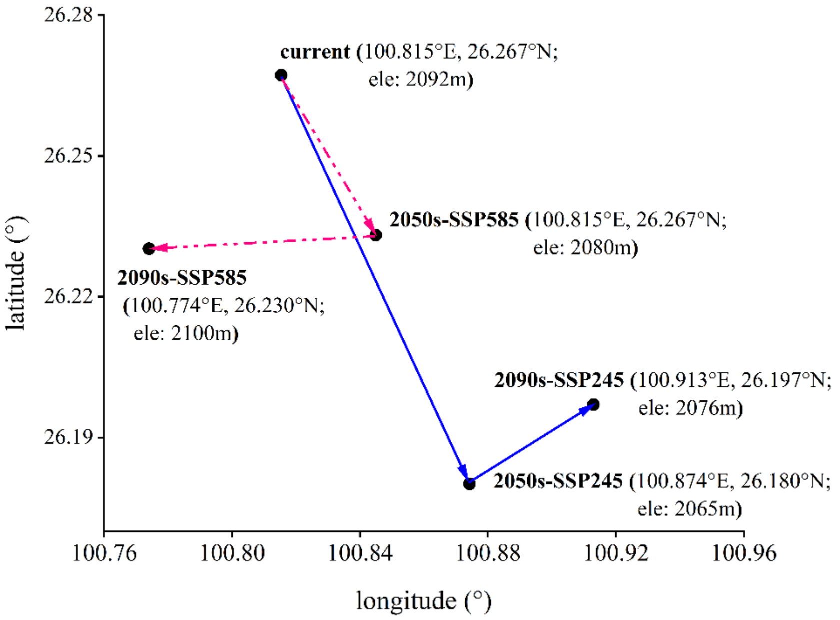


Figure 7. *Shifts in potential habitats of P. yunnanensis under different periods and climate scenarios*

Discussion

The influence of climate change on species habitat shifts is an extremely complex dynamic process. Understanding how future climate change will shape species distribution and diversity, and how it will drive shifts in species range, is an urgent task (Santini et al., 2021). Mountainous species are more vulnerable to extinction in the context of climate warming due to their restricted geographic distribution (Ahmadi et al., 2019) and slow adaptive evolution. Southwestern China has a mild climate and moderate seasonality in temperature, making it an ideal refugia for coniferous species in addition to being a global conifer-endemic hotspot (Liang et al., 2018; Tang et al., 2018; Dakhil et al., 2021). However, global warming is expected to pose a serious threat to coniferous forests in this region (Dakhil et al., 2019). Here, based on a large number of species occurrence records, we attempt to investigate potential suitable habitats and range shifts of *P. yunnanensis* in response to future climate change, and further explore the associated driving mechanisms. Our results show a general decline in suitable habitats under most climate scenarios, which is coincident with previous findings that global warming leads to habitat loss (Zhang et al., 2014). Shifts in species distributional ranges are critical to maintaining local biodiversity. As a dominant species in temperate coniferous communities, the losses of suitable habitats for *P. yunnanensis* would undoubtedly have a negative impact on functions and services of forest ecosystem.

In general, climate change affects species distribution through direct impacts on species physiological tolerances and indirect effects on the resource availability for plant growth (Fuller et al., 2016). As proxies for actual limiting resources, bioclimatic variables are reliably used to assess possible shifts in species ranges under future warming (van Beest et al., 2021), although their importance in predicting the distribution of conifer species are different (Dakhil et al., 2021). According to our projections, the shifts in suitable habitats of *P. yunnanensis* are primarily driven by temperature-related variables, particularly temperature seasonality (bio4), minimum temperature of coldest month (bio6) and mean diurnal range (bio3), indicating that *P. yunnanensis* is very sensitive to temperature variability. This result is in accordance with those of recent studies confirming the importance of temperature seasonality on the growth and development rhythms of plants (Xie et al., 2022), especially for pine species (Naudiyal et al., 2021). Our results also reveal that too large (>550) or too small (<380) temperature variations are not conducive to growth, indicating a narrow ranges of optimum temperature variation for *P. yunnanensis*. These results are consistent with the findings of Dakhil et al. (2021). Stable and less seasonal climates increase species richness (Gomes et al., 2020), while increasing temperature variability associated with climate change would lead to species loss (Zhang et al., 2014). A considerable increase in temperature seasonality in some areas of southwestern China (Zhang et al., 2014) may partially explain the reduction in suitable habitats for *P. yunnanensis* under future climate scenarios. In addition, *P. yunnanensis* is restricted to areas with min temperature of coldest month between −7.5 °C and 6 °C, as these temperatures are likely to be the optimal range for *P. yunnanensis* to grow. Moreover, our study shows that although the distribution of *P. yunnanensis* is driven by temperature-related variables most, the influence of solar radiation cannot be ignored, as it is a major source of photothermal energy for the Earth’s ecosystems and indirectly affects precipitation and temperature patterns on the Earth’s surface. Therefore, our results support the theory proposed by Palmer et al. (2015) and Li and Park (2020) that species range shifts are largely dependent on thermal niche. Similarly, several studies conducted in southwestern China (e.g., Dakhil et al., 2021; Dang et al., 2021) have demonstrated that minimum temperature of the coldest month and temperature seasonality are important determinants for the growth and distributions of temperate coniferous forests, as well as for tree species richness. Increased evapotranspiration due to continued future warming could eventually increase forest vulnerability in this region (Sun et al., 2022).

It is worth noting that precipitation-related variables (e.g., bio14, bio15 and bio19) have a weaker influence on suitable habitat shifts, which are probably related to the abundant rainfall caused by the East Asian monsoon in southwestern China (Tong et al., 2016). Thus, precipitation is no longer a limiting factor for species distribution in this region. Our study also confirms the findings of Dakhil et al. (2019) and Liao et al. (2019) that the influences of temperature and solar radiation on coniferous forests were stronger than that of precipitation in southwestern China. With respect to edaphic factors, soil type was more influential than soil texture on range shifts of *P. yunnanensis*, which may be attributed to soil nutrients between different soil types. Changes in soil conditions limit upslope movements of species in response to climate change (Brown and Vellend, 2014). Overall, bioclimatic variables in our study are more important than topo-soil variables in explaining the distribution of *P. yunnanensis*.

Species habitat contractions associated with climate change appears to be common. This is also reflected in vegetation dynamics, such as continuous warming lead to a decrease in vegetation cover in the southern Hengduan Mountains and high-elevation areas of northwestern Yunnan (Yin et al., 2020; Huo and Sun, 2021). In the present study, obvious decreases of 2.80% (under SSP245) and 4.22% (under SSP585) in habitat area were observed for *P. yunnanensis* by the 2090s, indicating a clear acceleration of habitat loss with the severity of the SSP scenarios. Similar results are found in several studies (Li and Park, 2020; Dang et al., 2021). One possible explanation is that extreme temperatures under severe emission scenario limit species survival (Dakhil et al., 2021).

In addition to range contraction, rising temperatures over the past few decades have also changed the latitudes and altitudes of many species, especially those that occurred in alpine regions (IPCC, 2013). Although species range shifts in response to climate change are multidirectional (Boisvert-Marsh et al., 2014; Williams and Blois, 2018), poleward and upslope movements have been well documented (Liang et al., 2018; Liao et al., 2019; van Beest et al., 2021). Climatic factors such as seasonality, which usually vary along latitudinal gradients (Freeman et al., 2018), may explain this phenomenon to some extent. In our study, *P. yunnanensis* had a slightly southward and downslope shift in addition to range contraction, which may be related to its physiological traits such as habitat preference. Similar results are recorded in coniferous and temperate forests (Joshi et al., 2012; Naudiyal et al., 2021). The response patterns of species to climate change are species-specific (Boisvert-Marsh et al., 2014; He et al., 2019) and can be better described by species traits (Williams and Blois, 2018). For example, as one of the representative species of warm coniferous forests in southwestern China (Dakhil et al., 2019), *Pinus* species prefer low-mid altitude habitats, which was verified in our study. Mountainous species are mostly distributed under specific abiotic conditions and therefore have very limited opportunities to avoid climate change by migrating to higher elevations or latitudes. In addition, there are many other factors that hinder species from migrating upwards, such as the "summit traps" phenomena (Pertoldi and Bach, 2007) and susceptibility to cold climatic conditions (Rana et al., 2021), which may result in a lack of suitable alpine habitats for further expansion of mountainous species. Moreover, as a strong driver of species range shifts, microclimate arising from complex topography in mountain ecosystems may partially buffer species against poleward and upslope movements as well as macroclimatic change (Suggitt et al., 2018; Křenová et al., 2022).

Migration direction of species has been proved to be related to their location (Liao et al., 2019). The large increase in both elevation and latitude from south to north in southwestern China give rise to limited northward expansion of species range caused by climate change, consequently, most woody plants will lose suitable habitat range because they have difficulty moving northward to track climate warming (Zhang et al., 2014). Körner (2021) and Qian et al. (2022) showed that northern range limits of plant species in North Hemisphere is strongly associated with minimum temperature of the coldest month and temperature seasonality, where temperature seasonality constrains the expansion of species ranges (Wiens et al., 2006). Moreover, unique geography of the region, with a gradual rise in elevation from south to north, may result in a slight southward shift in species ranges. Our projection on species migration direction was also supported by Boisvert-Marsh et al. (2014), who found that southward movement exists in *Abies* and *Picea* forests in North America. According to Freeman et al. (2021), adaptation, rather than elevational shifts, may be the key processes to the response of

DOI: http://dx.doi.org/10.15666/aeer/2101_041058

temperate mountainous species to continued warming, as their range shifts lag far behind climate change.

Under future climate scenarios, southern Sichuan and northern Yunnan are expected to be the most suitable and stable regions to support the occurrence of *P. yunnanensis* and can serve as a refuge, although these areas have been identified as climate-sensitive areas for dark coniferous forests (Liao et al., 2019). Furthermore, although the distribution range of *P. yunnanensis* covers a broad geographic area of the study area, the most critical conservation priority areas should focus on southeastern Tibet, as the current suitable habitats in this region will obviously decrease under future warming, indicating that *P. yunnanensis* in southeastern Tibet seems to be more threatened by climate change. This agrees well with the view of Sun et al. (2022) that coniferous forests on the southeast Tibetan mountains are adapted to humid climates and thus are more sensitive to increasing drought trends. According to model projections, areas with potential losses of suitable habitat for the target species should be assumed as priority areas for in-situ conservation management, especially in central and western Sichuan and southeastern Tibet. This is consistent with the results of Wan et al. (2017) and Sun et al. (2022), who proposed Sichuan and Tibet as priority conservation areas for coniferous forests under climate change since these areas are expected to become less suitable under the future climate scenarios.

Although environmental changes have a strong influence on the distribution and shift of *P. yunnanensis*, other potential drivers such as biotic interactions, geographic barriers, dispersal ability and adaption of species, and human activities should not be ignored. For example, extreme climatic events can adversely affect reproduction of plants, especially those grown at high altitudes (Křenová et al., 2022). In addition, climate data resolution has a large impact on uncertainty in projections of species range (Thuiller et al., 2019; Brun et al., 2020). Compared to high-resolution climate data, coarse-resolution climate data are more difficult to account for fine-scale variations in climate and therefore may overestimate species range shifts (Suggitt et al., 2018). Although dispersal is an effective way for species to cope with the effects of climate change, long-distance dispersal is typically rare for woody species (Corlett, 2009) because of their physiological characteristics such as large mass, size, and slow growth, which make them hardly keep up with the pace of future climate change. In addition, complex geographic barriers in southwestern China, such as high mountains (e.g., Hengduan Mountains) and Asian rivers (e.g., Yangtze, Mekong, and Salween rivers), may block many species from reaching suitable habitats; this is not conducive to the spread of tree seeds (Li et al., 2021). Consequently, there will be a contraction in distribution ranges of *P. yunnanensis* in the case of limited natural migration. The results of Dakhil et al. (2021) also confirmed that the suitable areas of endemic conifer species in southwestern China would continue to decrease under global climate change. Topographic heterogeneity can create stable climatic conditions that reduce extinction risk for plant species by buffering regional climate variability (Suggitt et al., 2018; Tang et al., 2018; Mamantov et al., 2021), especially in southwestern China, where more suitable local habitats provided by complex terrain effectively support species survival under rapid environmental change (Li et al., 2021). Therefore, our results supported the projection of Liang et al. (2018) that numerous montane plants in the Hengduan Mountains may not be at high risks of drastic range contraction or even extinction due to future climate warming, further supporting the view that the mountainous regions of southwestern China will remain a long-term stable refuge in the future (Tang et al., 2018).

Despite these limitations, our study provides valid evidence that the reduced distribution range and slight southward shifts of *P. yunnanensis* is most likely a response to global warming. Therefore, we should pay special attention to the species habitat losses and range shifts due to complex interplay among climate-related factors, biotic variables, species-specific traits (e.g., thermal tolerance), and human activities in the context of increasing global warming. This is of great significance for species conservation and strategy making in biodiversity hotspots under global change.

Conclusions

Our study predicted range shifts in the distribution of *P. yunnanensis* in southwestern China based on two climate scenarios, providing important insights for understanding the responses of endemic species to future climate change. We found that suitable habitat for *P. yunnanensis* tended to contract and shift slightly southward under ongoing climate change, primarily driven by temperature-related variables and solar radiation, with less influences from precipitation and other environmental factors. In addition, there was a clear acceleration of habitat losses with the severity of climate scenarios. Our results suggested that southern Sichuan and north-central Yunnan could serve as long-term refuges for *P. yunnanensis* under future climate change, while southeastern Tibet should be protected as priority conservation areas, although montane species in this region may not be at high risk of drastic range contraction. In further research, a broader set of variables with high-resolution should be incorporated into modelling approach to better assess the potential impacts of future climate changes on suitable habitats for mountainous coniferous species, as species distribution dynamics are probably the result of synergistic effects of different mechanisms.

Acknowledgments. The authors thank the anonymous reviewers for their constructive comments on our manuscript. This study was funded by the Special Basic Cooperative Research Programs of Yunnan Provincial Undergraduate Universities' Association (2018FH001−104) and the Talent Introduction Project of Kunming University (YJL18018).

Conflict of interests. The authors declare that there is no conflict of interests regarding the publication of this paper.

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