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Prediction of future potential distributions of *Pinus yunnanensis* varieties under climate change

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Pinus yunnanensis Franch. (Pinaceae) is an important endemic tree species that serves as a critical constituent of the forest ecosystems and plays a significant role in forestry economic production in southwest China. *P. yunnanensis* comprises three varieties: var. *yunnanensis,* var. *pygmaea* and var. *tenuifolia,* with significant variation in traits, such as height and leaf size. This study aims to characterize the habitat conditions of the three varieties and predict their potential future distributions by employing MaxEnt model. Temperature seasonality (BIO4) emerged as the most influential factor affecting the distribution of var. *yunnanensis*; isothermally (BIO3) stands out as the most critical factor for the distribution of var. *pygmaea*; whereas mean annual fire occurrence (MAF) had the greatest impact on the distribution of var. *tenuifolia*. Under future climate conditions, the highly and moderately suitable habitats for all the three varieties are projected to decrease, while the lowly suitable habitats are projected to increase. The distribution centroids of all the three varieties are anticipated to shift to higher latitudes. Our study characterized the habitat conditions and predicted the potential future distribution of the three *Pinus yunnanensis* varieties, which could help the conservation and utilization of *Pinus yunnanensis* varieties.

KEYWORDS

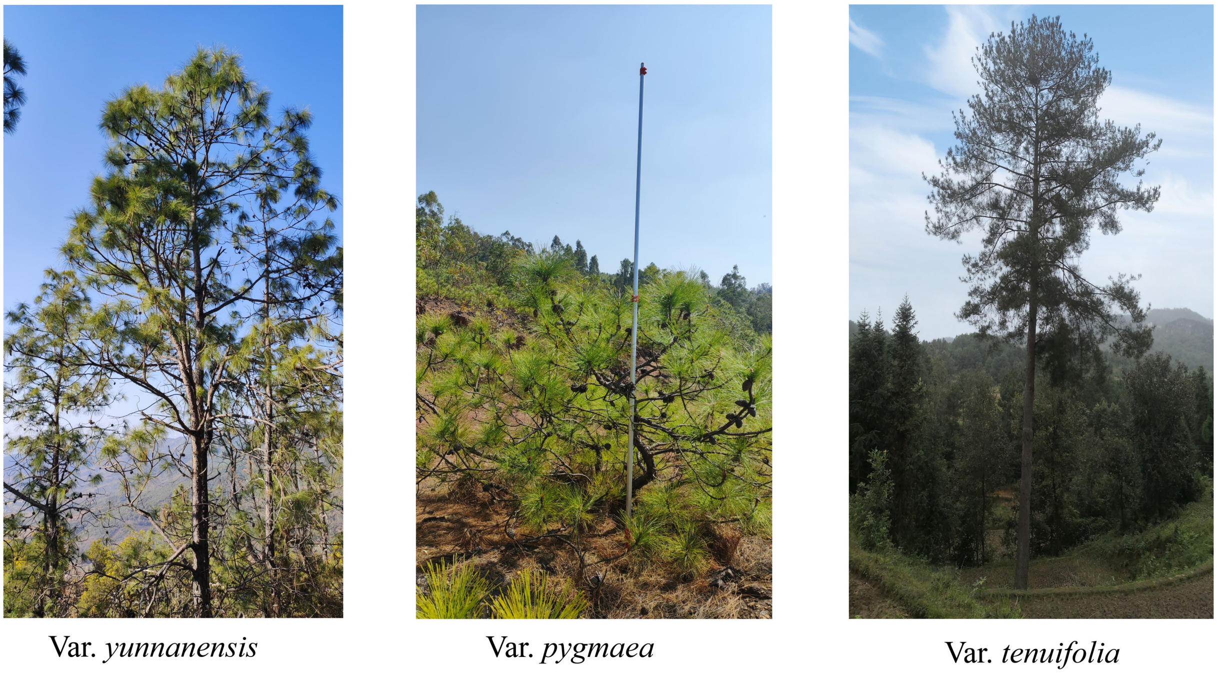
***Pinus yunnanensis*, MaxEnt model, distribution, climate change, habitat conditions**

1 Introduction

Pinus yunnanensis Franch. (Pinaceae) is a unique species that only can be found in southwest China (Wang et al., 2013), but also one of the most widespread species in this region. The *P. yunnanensis* forest is highly regarded in forestry production due to its high resin content and wood quality. Furthermore, it plays a crucial role in the ecological development of the Yangtze and Jinsha River basins (Cai et al., 2016). There are three varieties (var. *yunnanensis*, var. *pygmaea* and var. *tenuifolia*) in *P. yunnanensis*, and the three varieties showed considerable variations in traits (Sun et al., 2020). For example, var. *yunnanensis* and var. *tenuifolia* are trees, generally can grow above 15 m, while var. *pygmaea* is a dwarf shrub that typically grows no taller than 2–3 meters, hence it is not suitable for timber production (Figure 1). The length of var. *yunnanensis* leaves usually ranges from 10 to 30 cm, while the var. *pygmaea* has shorter leaves ranging from 7 to 13 cm; var. *tenuifolia* has the longest leaves, which can reach up to 36 cm (Flora Reipublicae Popularis Sanicae: http://frps.iplant.cn/). *P. yunnanensis* varieties also exhibit great variation in habitat conditions: var. *yunnanensis* grows at altitudes of 1,000–3,200 m elevation and occupies diverse habitats; var. *pygmaea* usually grows on dry and barren, sunny upper slopes, at altitudes of 2,200–3,100 m elevation; while var. *tenuifolia* grows at altitudes of 400–1,200 m elevation, along riversides (Chen et al., 2021). Exploring the variations in traits and habitat conditions across the three varieties can provide insight into evolutionary process of *P. yunnanensis*. *P. yunnanensis* growing in different environments displays substantial variations in its growth, which is attributed to variations in precipitation, temperature, and elevation (Zhou et al., 2022). Therefore, the variations in environmental conditions significantly impact timber production of *P. yunnanensis* (Shen et al., 2020). However, the exactly variation of habitat conditions and distribution across the three varieties are still unclear. What environmental factors are important influencers on their geographic distribution, and how climate change will affect the distribution of *P. yunnanensis*, thus affecting timber production, also have been scarcely studied.

Under climate changing, the risk of forest fires has become increasingly severe, posing a serious threat to global timber production (Bousfield et al., 2023). The southwestern region of China, where *P. yunnanensis* is situated, is prone to frequent wildfires. This has led to the development of varying adaptive strategies for dealing with different fire environments (Tang et al., 2013). Therefore, in addition to bioclimatic environmental variables, wildfires, as a significant environmental factor, may also influence the distribution of *P. yunnanensis* and its variants. Currently, there is limited research on this aspect, especially considering wildfires as an impacting variable. Consequently, gaining insights into the impacts of climate change and wildfires on the distribution of *P. yunnanensis* is paramount for formulating nuanced forest management policies aimed at the preservation and sustainable utilization of this species.

Climate change has great impacts on species distribution, ecosystem structure and biological community composition (Root et al., 2003; Huang et al., 2022; Ouyang et al., 2022). Many studies have showed that climate change will cause considerable changes in the distribution of plant species (Ji et al., 2020; Ab Lah et al., 2021; Zhang et al., 2021; Li et al., 2023). For example, *Kalanchoe* × *houghtonii* (Crassulaceae) is an invasive species that has rapidly expanded in recent years. To explore its distribution pattern, Herrando-Moraira et al. (2020) used the MaxEnt model to predict its future distribution and discussed the crucial variables influencing its distribution. *Leucanthemum vulgare* (ox-eye Daisy) is an invasive species with a wide global distribution, Ahmad et al. (2019) utilized species distribution models to predict the future distribution of *Leucanthemum vulgare* (ox-eye Daisy), enabling early detection of areas susceptible to invasion and preventing further spread of the species. Prediction of the potential distribution of regional species also been reported. For example, Ferreira et al. (2016) projected that 90% of the 206 local species on oceanic islands (Azores) would lose their climatic space in future. Similarly, *Akebia trifoliata* (Ranunculaceae) is a fruit found mainly in southern China, Zhang et al. (2022) employed the MaxEnt model to predict the distribution of wild *Akebia trifoliata* (Ranunculaceae), under different future climate scenarios and observed a shift of suitable habitat from south to north. Hu et al. (2019) examined the impact of climatic changes on the distribution patterns of six typical *Kobresia* forage species in the Tibetan Plateau, and found that climate warming would create unfavorable survival conditions for



Var. *yunnanensis* Var. *pygmaea* Var. *tenuifolia*

FIGURE 1
Photographs of var. *yunnanensis*, var. *pygmaea* and var. *tenuifolia*. The height of the stick next to var. *pygmaea* in the figure is 4.5 m.

these species, resulting in their degradation. Predicting future distribution of plant species can facilitate understanding of the relationship between climate change and species distribution patterns, thereby guiding conservation measures.

Species distribution model (SDM) is developed on the basis of niche theory (Guisan and Thuiller, 2005), which is widely used to predict species distribution (Zhang et al., 2021; Li et al., 2022). It is a model that associates the distribution of the target species with the relevant environmental factors to calculate the ecological requirements for the distribution of the species through the algorithm, and to predict the potential distribution of the species in a certain area under specific space–time conditions (Elith et al., 2011; Dyderski et al., 2018). Currently, commonly used species distribution modeling (SDM) models include the bioclimatic model (BIOCLIM), ecological niche factor analysis model (ENFA), genetic algorithm for rule-set production model (GARP), and maximum entropy model (MaxEnt) (Tsoar et al., 2007; Bradie and Leung, 2017). The MaxEnt model offers several advantages, such as the ability to select control variables, estimate coefficients for environmental variables, and visualize analysis results effectively. Notably, the MaxEnt model incorporates a response curve function for each variable, providing a more intuitive representation of the threshold range of a single environmental factor's impact on species distribution (Parveen et al., 2022). In addition, the MaxEnt model demonstrates high accuracy in predicting species distribution, particularly for species with small sample sizes and relatively concentrated distributions, thus making it as one of the most reliable SDM models (Wang et al., 2021; Huang et al., 2022).

Pinus yunnanensis Franch. (Pinaceae) is an important endemic tree species that serves as a critical constituent of the forest ecosystems and plays a significant role in forestry economic production in southwest China. However, the distribution of *P. yunnanensis*, especially the variation in distribution across its three varieties, has been scarcely studied. How the distribution of the three varieties will change under climate change is also unclear. In this study, we aim to predict both the present and future distribution patterns of *P. yunnanensis* varieties by employing the MaxEnt model, and to unravel the key environmental variables that exert significant influences on their distribution. The objectives of our research are: (1) To characterize the variation in the habitat conditions of the 3 *P. yunnanensis* varieties; (2) To identify the key environmental factors that has influenced the distribution of the 3 *P. yunnanensis* varieties; (3) To predict the current and future distribution areas of the 3 *P. yunnanensis* varieties (4) To elucidate the shifts of the distribution centers of the 3 *P. yunnanensis* varieties. We hope our study can facilitate the conservation and sustainable utilization of *P. yunnanensis*, and guide the management of *P. yunnanensis* forests.

2 Methods

2.1 Study area

This study was conducted in the southwestern region of China, including Sichuan, Yunnan, Guizhou, and Chongqing, Qinghai provinces and Tibet Autonomous Region, with a geographic range from 78°25′ to 112°08′ E longitude and 21°08′ to 36°19′ N latitude. Climate types in this region are diverse. For example, the Sichuan Basin has a mid-subtropical monsoon climate, the Yunnan-Guizhou Plateau has a south-central subtropical monsoon climate, and the mountains of the Qinghai-Tibet Plateau have a highland mountain climate. The average annual temperature in the southwest is about 16.5°C (Tang et al., 2021). The total annual precipitation in the southwest region is between 600 and 2,300 mm, mainly presenting a spatial distribution pattern of more precipitation in the east and less in the west, with more in the south and less in the north, accompanied by large differences in intra-annual distribution and distinct wet and dry seasons. *Pinus yunnanensis* were mainly distributed in Yunnan-Guizhou Plateau, where has a subtropical monsoon climate with alternating warm dry season and hot wet seasons, creating conditions that favour wildfires (Wu et al., 2020).

2.2 Collection of occurrence records for the three *Pinus yunnanensis* varieties

Pinus yunnanensis Franch. (Pinaceae) is one of the most widespread indigenous tree species in south-west China (Chen et al., 2021). The occurrence records for *P. yunnanensis* varieties are mainly derived from China forest and grassland fire risk survey. A total of 681 occurrences with coordinate information (var. *yunnanensis*: 630; var. *pygmaea*: 32; var. *tenuifolia*: 19) were obtained (Supplementary Table S1; Figure 2). The occurrence records of the three varieties vary greatly, but the number of occurrence records for each variety is roughly correlated with its distribution range. Var. *yunnanensis* has the widest distribution, predominantly abundant in Yunnan and Sichuan, with scattered occurrences in Guangxi, Guizhou, Tibet. Var. *pygmaea* follows with a significantly smaller distribution, limited to the central part of Yunnan and southern Sichuan. Var. *tenuifolia* has the smallest distribution across the three varieties and exists only at the tri-provincial border of Guangxi, Guizhou, and Yunnan.

2.3 Environmental data collection and data analysis

Nineteen bioclimatic variables data and altitude data were obtained from the World Climate Database (WorldClim: https://www.worldclim.org/). Wildfire data were obtained from the moderate resolution imaging spectroradiometer (MODIS) products of The fire information for resource management system (FIRMS: https://firms.modaps.eosdis.nasa.gov/). The mean annual fire occurrence from 2001 to 2021 were extracted at a grid cell size of 1 km × 1 km. Soil data, including nitrogen content, organic carbon content, sandy soil content and soil silt content of 0-5 cm soil, were obtained from Soilgrids (https://soilgrids.org/) (Poggio et al., 2021). Finally, we gathered data for 25 environmental variables, all of which are at a resolution of 30″ (Table 1). The variations in these variables among the three varieties were analyzed using a one-way analysis of variance in SPSS (IBM Corp, 2013). To assess whether there are significant differences in environmental variables among the three varieties statistically, the Least Significant Difference (LSD) method was employed to ascertain the significance of differences among these three varieties. For the prediction of further distribution of *P. yunnanensis*, we selected the global bioclimatic data under the shared socio-economic pathways SSP1-2.6 and SSP5-8.5 in the BCC-CSM2-MR atmospheric circulation model from 2040 to 2060 and 2060–2080 (Séférian et al., 2019). Because *P. yunnanensis* is mainly distributed in the southwest of China, the environment variables are cut to the southwest using ArcGIS10.8 and convert it to ASC II format that can be recognized by MaxEnt software.

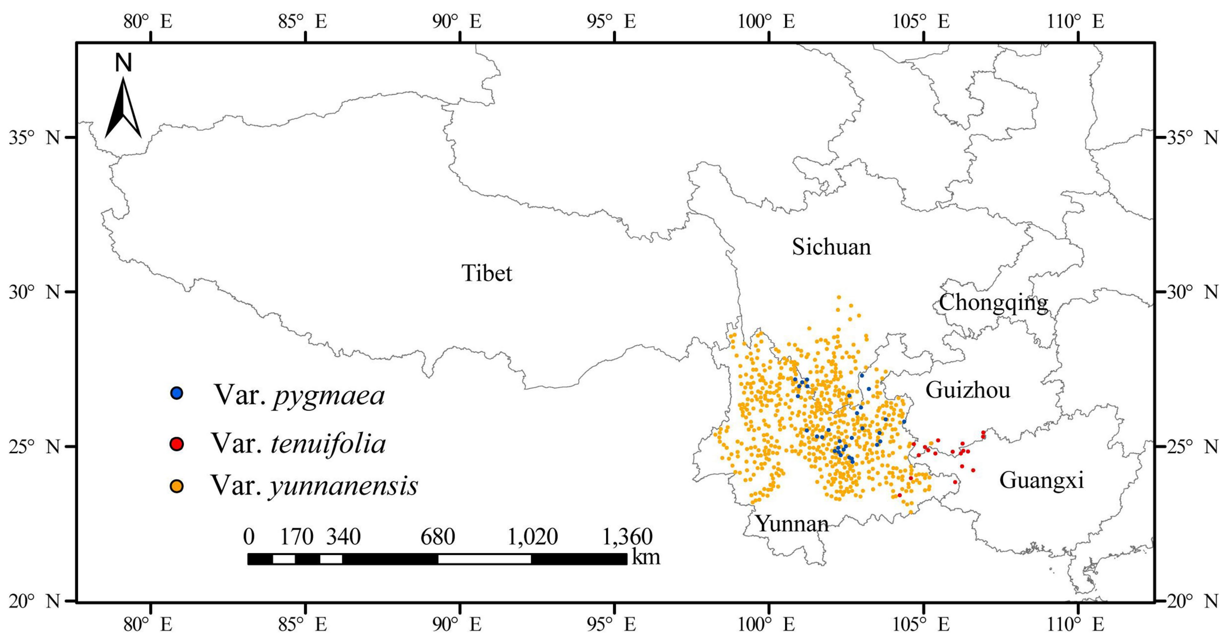


FIGURE 2
The occurrence records of the three *Pinus yunnanensis* varieties.

TABLE 1 The sources for the environmental variables in this study.

Environment variable	Source	Dataset type	Resolution
Elevation	https://www.worldclim.org/	Geotiff	30″
Mean annual fire occurrence	https://firms.modaps.eosdis.nasa.gov/	Shapefile	30″
Soil nitrogen content in 0–5 cm	https://soilgrids.org/	Geotiff	30″
Soil sand content in 0–5 cm	https://soilgrids.org/	Geotiff	30″
Soil silt content in 0–5 cm	https://soilgrids.org/	Geotiff	30″
Soil soc. content in 0–5 cm	https://soilgrids.org/	Geotiff	30″
Current 19 bioclimatic variables (BIO1-BIO19)	https://www.worldclim.org/	Geotiff	30″
Future 19 bioclimatic variables (BIO1-BIO19)	https://www.worldclim.org/	Geotiff	30”

2.4 MaxEnt model construction and result evaluation

We employed MaxEnt software (version 3.4.1) to develop the model, specifying a maximum of 500 iterations. We randomly assigned 25% of the species distribution points as the test dataset, while the remaining 75% were used as the training dataset. To assess the contribution and importance of each variable to the model construction, we conducted jackknife analysis (Fand et al., 2020; Baradevanal et al., 2023; Ullah et al., 2023). Additionally, we utilized the response curve function to determine the threshold range of the impact of individual environmental variables on the distribution of *P. yunnanensis*. Other model parameters were set to their default values, and the entire process was repeated 10 times. The final output of the model was imported into ArcGIS 10.8. To classify the distribution probability of the species, we employed the reclass tool to assign four grades ranging from 0 to 1: 0–0.1 represents unsuitable habitats, 0.1–0.4 represents lowly suitable habitats, 0.4–0.7 indicates moderately suitable habitats, and 0.7–1.0 represents highly suitable habitats.

The shift of distribution centers for the three varieties in future periods was analyzed by using the SDM toolbox, a Python-based tool for ArcGIS. After inputting files containing the model-predicted future species habitat and the current habitat, a vector file (line) is generated. This file illustrates the movement of the distribution center of each variety from the current center to a specific location in the future period.

The accuracy of the model is evaluated by Receiver Operating Characteristic (ROC) analysis (Merow et al., 2013). It is a method employed by MaxEnt software to assess model accuracy, with the Area Under the ROC Curve (AUC) serving as the evaluation metric (Phillips et al., 2006). One advantage is that the AUC provides a standardized measure of model performance, independent of the choice of any threshold. This metric is widely utilized in the evaluation of species distribution models (Phillips and Dudík, 2008). An AUC value exceeding 0.9 indicates excellent model accuracy, while an AUC above 0.8 suggests good model prediction. AUC values between 0.7 and 0.8 indicate moderate model accuracy. However, if the AUC value falls within the range of 0.5 to 0.6, the model's predictions are considered to

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be unsuccessful. A flowchart of the methodology in this study was provide to illustrate the steps (Figure 3).

3 Results

3.1 Habitat conditions varied significantly across the three *Pinus yunnanensis* varieties

Among the three varieties of *P. yunnanensis*, significant differences in habitat conditions were observed across var. *tenuifolia*, var. *yunnanensis* and var. *pygmaea* (Table 2). Var. *tenuifolia* exhibited an average annual temperature of 17.9°C and an annual precipitation of 1262.1 mm, significantly higher than the other two varieties. Var. *tenuifolia* experienced a higher frequency of annual wildfires, while its elevation was significantly lower than that of var. *yunnanensis* and var. *pygmaea*. Based on the results, the habitat conditions of var. *yunnanensis* and var. *pygmaea* are generally consistent, with both species growing in higher elevations characterized by lower temperatures and precipitation. In contrast, var. *tenuifolia* thrives in lower elevations, in regions that are warmer and more humid.

3.2 Important environmental variables for the current distribution of the three *Pinus yunnanensis* varieties

The contribution rate of each environmental variable (for all the 25 variables) to the distribution of *P. yunnanensis* varieties were evaluated by using the jackknife method (Table 3). The main environmental variables that affected the potential distribution of var. *yunnanensis* are temperature seasonality (BIO4, 32.4%), mean

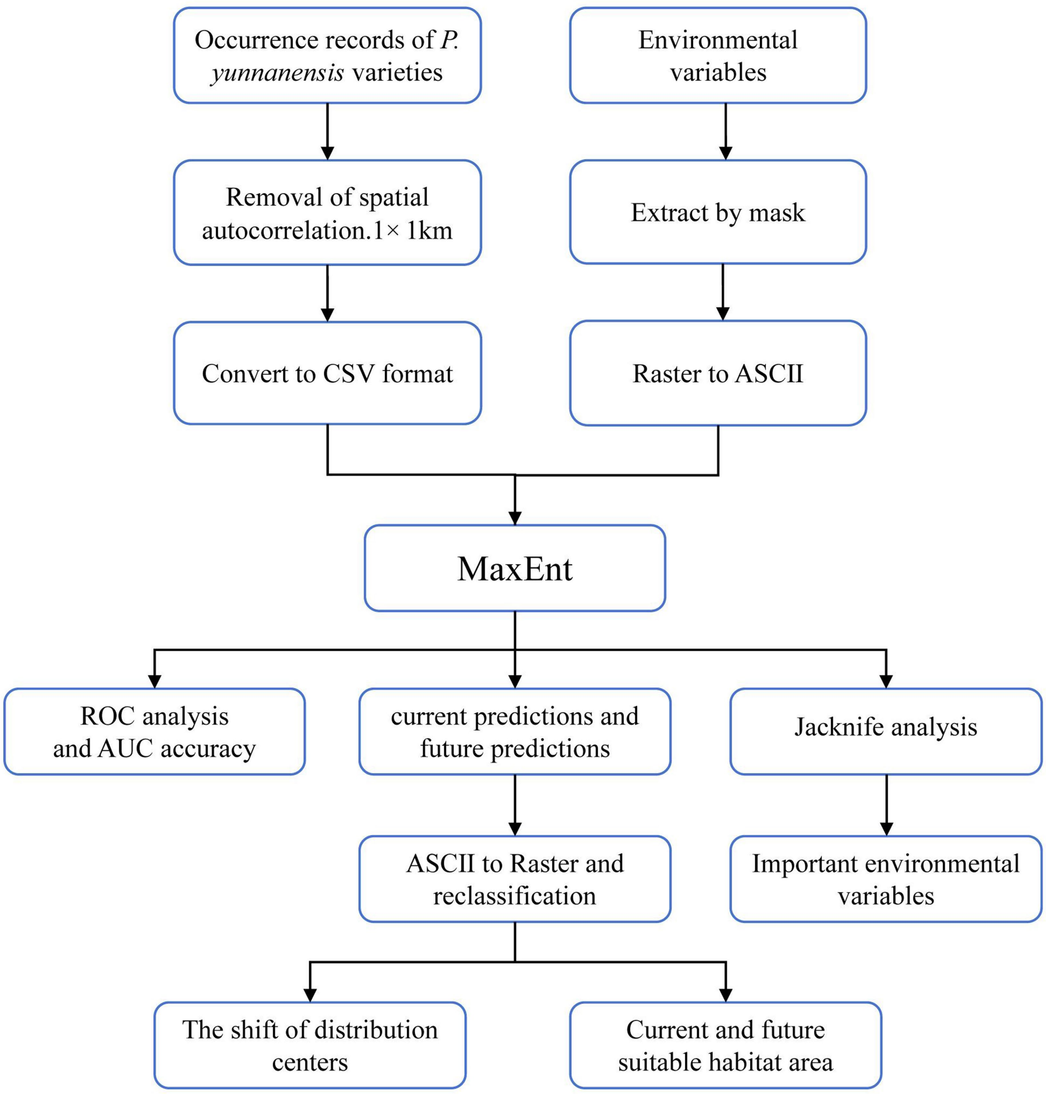

FIGURE 3
Flowchart of the methodology adopted in this study.

TABLE 2 Differences in habitat conditions among the three *Pinus yunnanensis* varieties.

Environment variable	Description	Var. *yunnanensis*	Var. *pygmaea*	Var. *tenuifolia*
BIO1	Annual mean temperature (°C)	14.448 ± 2.783 b	13.289 ± 2.849 b	17.916 ± 1.573 a
BIO2	Mean diurnal range [mean of monthly (max temp-min temp)] (°C)	10.873 ± 0.771 a	11.126 ± 0.639 a	8.465 ± 0.533 b
BIO3	Isothermally (Bio2/Bio7) (×100)	46.459 ± 2.738 a	47.142 ± 1.621 a	36.624 ± 3.309 b
BIO4	Temperature seasonality (standard deviation×100)	466.410 ± 43.059 b	461.113 ± 22.378 b	562.159 ± 42.308 a
BIO5	Max temperature of warmest month (°C)	24.213 ± 2.455 b	23.062 ± 2.972 b	28.394 ± 1.748 a
BIO6	Min temperature of coldest month (°C)	0.790 ± 3.069 b	−0.534 ± 2.734 b	5.2159 ± 1.794 a
BIO7	Temperature annual range (Bio5–Bio6) (°C)	23.423 ± 1.305 a	23.596 ± 0.964 a	23.178 ± 0.994 a
BIO8	Mean temperature of wettest quarter (°C)	19.477 ± 2.332 b	18.226 ± 2.600 c	23.967 ± 1.719 a
BIO9	Mean temperature of driest quarter (°C)	8.415 ± 3.060 b	7.106 ± 2.860 b	10.301 ± 1.618 a
BIO10	Mean temperature of warmest quarter (°C)	19.485 ± 2.323 c	18.229 ± 2.604 b	24.085 ± 1.668 a
BIO11	Mean temperature of coldest quarter (°C)	8.194 ± 3.076 b	7.090 ± 2.876 b	10.301 ± 1.618 a
BIO12	Annual precipitation (mm)	949.677 ± 163.355 b	888.750 ± 82.863 b	1262.052 ± 52.473 a
BIO13	Precipitation of wettest month (mm)	187.480 ± 37.962 b	177.125 ± 15.201 b	243.368 ± 16.859 a
BIO14	Precipitation of driest month (mm)	11.014 ± 3.200 b	10.375 ± 2.239 b	14.473 ± 3.421 a
BIO15	Precipitation seasonality (coefficient of variation)	81.733 ± 9.753 a	84.172 ± 3.985 a	81.909 ± 3.905 a
BIO16	Precipitation of wettest quarter (mm)	513.246 ± 103.857 b	488.750 ± 49.648 b	687.000 ± 42.391 a
BIO17	Precipitation of driest quarter (mm)	41.341 ± 12.973 b	36.656 ± 6.115 b	58.421 ± 8.002 a
BIO18	Precipitation of warmest quarter (mm)	511.733 ± 105.667 b	475.187 ± 67.351 b	684.684 ± 46.847 a
BIO19	Precipitation of coldest quarter (mm)	43.698 ± 16.151 b	36.656 ± 6.115 b	58.421 ± 8.002 a
MAF	Mean annual fire occurrence (times/year)	14.873 ± 13.399 b	9.962 ± 8.637 b	34.416 ± 21.260 a
NIT	Soil nitrogen content in 0–5 cm (g/kg)	4.167 ± 1.121 a	3.909 ± 1.171 a	2.863 ± 0.371 b
SAND	Soil sand content in 0–5 cm (%)	28.822 ± 5.985 b	24.968 ± 6.056 a	25.578 ± 3.877 b
SILT	Soil silt content in 0–5 cm (%)	41.006 ± 3.459 b	42.593 ± 2.993 ab	43.368 ± 2.338 a
SOC	Soil soc. content in 0–5 cm (%)	51.506 ± 13.378 a	48.037 ± 15.219 a	38.452 ± 3.975 b
ELEV	Elevation (m)	2091.696 ± 481.538 a	2302.281 ± 520.651 a	947.315 ± 332.951 b

Different lowercase letters indicate significant differences across varieties ($p < 0.05$); same lowercase letters indicate insignificant differences across varieties ($p > 0.05$).

annual fire occurrence (MAF, 22.2%), isothermality (BIO3, 19.1%), minus temperature of coldest month (BIO6, 9.2%) and elevation (ELEV, 8.8%), which contribute the most to the prediction model under current climate environment, and their total contribution rate reaches 91.7%; The main environmental variables that affected the potential distribution of var. *pygmaea* are isothermality (BIO3, 24.1%), mean annual fire occurrence (MAF, 18.6%), sandy soil content (SAND, 17.4%), temperature seasonality (BIO4, 13.2%), min temperature of coldest month (BIO6, 9%), and elevation (ELEV, 5.3%), with a total contribution rate of 87.6%; For var. *tenuifolia*, mean annual fire occurrence (MAF, 53.5%), isothermality (BIO3, 14.8%), soil nitrogen content (NIT, 9.9%), precision of driest month (BIO14, 8.2%), and elevation (ELEV, 7.6%) are the main environmental variables that have a cumulative contribution rate of 94%.

3.3 Current potential suitable habitat areas for the three *Pinus yunnanensis* varieties

The highly and moderately suitable area for var. *yunnanensis* span approximately 10.27×10^4 km^2 and 15.63×10^4 km^2, predominantly located in north-central Yunnan and southern Sichuan, ranging from 98.3–105.3° E and 23.3–28.8° N (Figure 4A1). Var. *pygmaea* exhibits a highly and moderate suitable area of around 2.12×10^4 km^2 and 3.95×10^4 km^2, mainly distributed in central Yunnan and along the Yunnan-Sichuan border, spanning from 100.1–104.1° E and 24.1–27.8° N (Figure 4B1). As for var. *tenuifolia*, the highly and moderately suitable area encompass approximately 2.84×10^4 km^2 and 3.21×10^4 km^2, with a primary distribution along the border of Guangxi, Yunnan, and Guizhou, ranging from 103.7–107.5° E and 23.2–25.8° N (Figure 4C1).

3.4 Future changes in suitable habitat areas for the three *Pinus yunnanensis* varieties

We conducted predictions on the future suitable habitat area for the three varieties under two shared socio-economic pathways for two future periods (Figure 4; Table 4). According to the future climate model, it is projected that the total habitat area for all three species will increase under both emission concentrations between 2040 and 2060. The variation in habitat range for var. *yunnanensis* and var. *pygmaea* is relatively small, while the suitable habitat area for var. *tenuifolia* has

TABLE 3 The contribution rate of each environmental variable in determining the distribution of the three *Pinus yunnanensis* varieties.

Environmental variable	Description	Contribution (%)		
		Var. *yunnanensis*	Var. *pygmaea*	Var. *tenuifolia*
BIO1	Annual mean temperature (°C)	0.2	0	0
BIO2	Mean diurnal range [mean of monthly (max temp-min temp)] (°C)	0.7	0.2	0.4
BIO3	Isothermally (Bio2/Bio7) (×100)	19.1	24.1	14.8
BIO4	Temperature seasonality (standard deviation×100)	32.4	13.2	0.7
BIO5	Max temperature of warmest month (°C)	0.7	0	0
BIO6	Min temperature of coldest month (°C)	9.2	9	0.1
BIO7	Temperature annual range (Bio5–Bio6) (°C)	0.4	0.2	0
BIO8	Mean temperature of wettest quarter (°C)	0.1	0.1	0
BIO9	Mean temperature of driest quarter (°C)	0	1	1.3
BIO10	Mean temperature of warmest quarter (°C)	0.1	0.2	0
BIO11	Mean temperature of coldest quarter (°C)	1.4	0.4	0
BIO12	Annual precipitation (mm)	2.2	0	0.4
BIO13	Precipitation of wettest month (mm)	0.2	0.1	0.1
BIO14	Precipitation of driest month (mm)	0.6	3.5	8.2
BIO15	Precipitation seasonality (coefficient of variation)	0	0.6	0
BIO16	Precipitation of wettest quarter (mm)	0.4	0.1	0
BIO17	Precipitation of driest quarter (mm)	0	1.6	0.4
BIO18	Precipitation of warmest quarter (mm)	0.1	0.7	1.4
BIO19	Precipitation of coldest quarter (mm)	0	1.8	0.6
MAF	Mean annual fire occurrence (times/year)	22.2	18.6	53.5
ELEV	Elevation (m)	8.8	5.3	7.6
NIT	Soil nitrogen content in 0–5 cm (g/kg)	0.2	0.5	9.9
SAND	Soil sand content in 0–5 cm (%)	0.4	17.4	0.2
SILT	Soil silt content in 0–5 cm (%)	0.1	0.3	0.2
SOC	Soil soc. content in 0–5 cm (%)	0.4	0.9	0.1

approximately doubled compared to the current climate. From 2060 to 2080, the total habitat area for the three species exhibited smaller change compared to the period of 2040–2060, with a tendency to become narrower. Over time, there is an overall increasing trend followed by a subsequent decreasing trend in the suitable habitat area for the three varieties.

Under the SSP1-2.6 climate scenario, the highly suitable area for var. *yunnanensis* is projected to be approximately $14.07 \times 10^4\,km^2$ during the period of 2040–2060, marking an increase of around 37% compared to the current distribution area. This highly suitable area is primarily concentrated in Yunnan and Sichuan. However, by 2060–2080, the highly suitable area decreases to $9.14 \times 10^4\,km^2$. The moderately suitable and lowly suitable areas for var. *yunnanensis* is projected to undergo minor changes. During 2060–2080, the highly suitable area and lowly suitable area of var. *yunnanensis* decrease by $4.93 \times 10^4\,km^2$ and $1.88 \times 10^4\,km^2$, respectively, compared to the period of 2040–2060. Meanwhile, the moderately suitable area increases by $1.61 \times 10^4\,km^2$. In the case of var. *pygmaea*, the highly suitable area is projected to be around $1.40 \times 10^4\,km^2$ from 2040 to 2060, indicating a decrease of approximately 33% compared to the current distribution area. This highly suitable area continues to decline to $0.90 \times 10^4\,km^2$ by 2060–2080. The moderately suitable area for var. *pygmaea* shows small changes under the SSP1-2.6 climate scenario, while the lowly suitable area experiences a slight increase, expanding toward southern Tibet in the future. For var. *tenuifolia*, the total suitable area increases by 18.1 × 104 km2 from 2040 to 2060, with a significant increase in the highly suitable area, which more than doubles. The lowly suitable area also expands by $13.31 \times 10^4\,km^2$. By 2060–2080, the suitable areas in higher latitudes for var. tenuifolia will decrease, resulting in a reduction of the total suitable area by $8.39 \times 10^4\,km^2$.

Under the SSP5-8.5 climate scenario, from 2040 to 2060, both the highly and moderately suitable areas of var. *yunnanensis* are projected to decrease by approximately 5%, while the lowly suitable area is expected to increase by 10%. The highly suitable area exhibits a significant decline in the period from 2060 to 2080, with a 73% decrease compared to 2040–2060, whereas the moderately and lowly suitable areas in Yunnan province will experience an increase (Figure 4). From 2040 to 2060, the highly suitable area for var. *pygmaea* is reduced by 74%. The moderately suitable area decreases by 8%, while the lowly suitable area increases by 38%. By 2060–2080, the highly and moderately suitable areas of var. *pygmaea* have nearly disappeared, with the emergence of lowly suitable areas in higher

TABLE 4 Predicted current and future suitable areas for the three *Pinus yunnanensis* varieties.

Species	Climate scenarios		Lowly suitable area (10^4 km^2)	Moderately suitable area (10^4 km^2)	Highly suitable area (10^4 km^2)	Total suitable area (10^4 km^2)
Var. *yunnanensis*	Current	1970–2000	17.717	15.630	10.268	43.614
	SSP1-2.6	2040–2060	18.374	14.440	14.072	46.886
	SSP5-8.5	2040–2060	19.654	14.721	9.695	44.070
	SSP1-2.6	2060–2080	16.490	16.057	9.149	41.696
	SSP5-8.5	2060–2080	23.011	19.303	2.580	44.894
Var. *pygmaea*	Current	1970–2000	9.376	3.950	2.124	15.450
	SSP1-2.6	2040–2060	11.108	3.387	1.405	15.900
	SSP5-8.5	2040–2060	12.950	3.596	0.553	17.098
	SSP1-2.6	2060–2080	12.908	3.629	0.904	17.440
	SSP5-8.5	2060–2080	12.693	0.423	0.013	13.130
Var. *tenuifolia*	Current	1970–2000	9.230	3.207	2.838	15.275
	SSP1-2.6	2040–2060	22.548	4.606	6.222	33.377
	SSP5-8.5	2040–2060	32.370	5.337	2.941	40.649
	SSP1-2.6	2060–2080	18.738	3.282	2.967	24.987
	SSP5-8.5	2060–2080	25.544	5.155	3.841	34.540

elevation regions, such as southern Tibet and parts of Sichuan. The total suitable area for var. *tenuifolia* undergoes an approximate 1.6-fold increase from 2040 to 2060, reaching an area of 40.64×10^4 km^2. Among them, the lowly suitable area demonstrates the most significant growth, with an increase of 23.14×10^4 km^2. The highly and moderately suitable areas also show an increase, albeit relatively small in terms of area. By 2060–2080, the total suitable area decreases by 6.11×10^4 km^2. The highly suitable area experiences a 30% increase, reaching 3.84×10^4 km^2, while the moderately suitable area and the lowly suitable area decrease by 3 and 21%, respectively. Under the high emission scenario SSP5-8.5, the high-suitability areas for the three varieties will significantly decrease. In 2060–2080, the high-suitability area for var. *pygmaea* will virtually disappear, which may be attributed to its narrower ecological niche.

3.5 The shift of the distribution centers for the three *Pinus yunnanensis* varieties

The sdmtoolbox within the ArcGIS software was utilized to analyze the alteration of distribution centers of *P. yunnanensis* varieties. Currently, the distribution center of var. *yunnanensis* is situated at 101.10° E and 25.83° N in Yunnan Province. However, the centroid of its distribution is projected to shift toward the northeast under future climate scenarios. Between 2040 and 2060, it is anticipated to relocate to 100.69° E and 26.00° N under the SSP1-2.6 scenario, and to 100.65° E and 26.36° N under the SSP5-8.5 scenario. By 2060–2080, the projected distribution center of var. *yunnanensis* is 100.80° E and 16.17° N under the SSP1-2.6 scenario, and 99.74° E and 26.97° N under the SSP5-8.5 scenario. The current distribution center of var. *pygmaea*, situated in Yunnan province, is situated at 101.97° E and 26.04° N. The distribution centers are anticipated to shift northward in the future. Between 2040 and 2060, it is anticipated to relocate to 101.91° E and 26.06° N under the SSP1-2.6 scenario, and to 101.57° E and 26.28° N under the SSP5-8.5 scenario. By 2060–2080, the projected distribution center of var. *pygmaea* is 100.80° E and 26.25° N under the SSP1-2.6 scenario, and 96.49° E and 27.88° N under the SSP5-8.5 scenario. The current distribution center of var. *tenuifolia* is situated at 105.14° E and 24.80° N in Guangxi province. Similarly, the centroid of its distribution is projected to shift toward the northwest in the future. Between 2040 and 2060, it is anticipated to relocate to 104.22° E and 26.19° N under the SSP1-2.6 scenario, and to 104.28° E and 27.01° N under the SSP5-8.5 scenario. By 2060–2080, the projected shift is 103.95° E and 25.89° N under the SSP1-2.6 scenario, and 103.75° E and 26.33° N under the SSP5-8.5 scenario. Our study showed that all the 3 *P. yunnanensis* varieties are likely to expand their range toward higher latitudes as temperatures rises. In future, the distribution range of the three varieties of *P. yunnanensis* is projected to shift northward, encompassing new habitats in Guizhou, Chongqing, and parts of Tibet that are currently outside their distribution range (Figure 5).

3.6 MaxEnt model accuracy verification

The MaxEnt model was utilized to predict the current potential distribution of the 3*P. yunnanensis* varieties in the current climate environment. The accuracy of models was evaluated by using the Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) values for the three species were 0.928, 0.982, and 0.984, respectively (Figure s1). All AUC values exceeded 0.9, indicating excellent accuracy in model's predictions.

4 Discussion

Environmental conditions shaped the distribution of plant species. We found that temperature-related factors played more

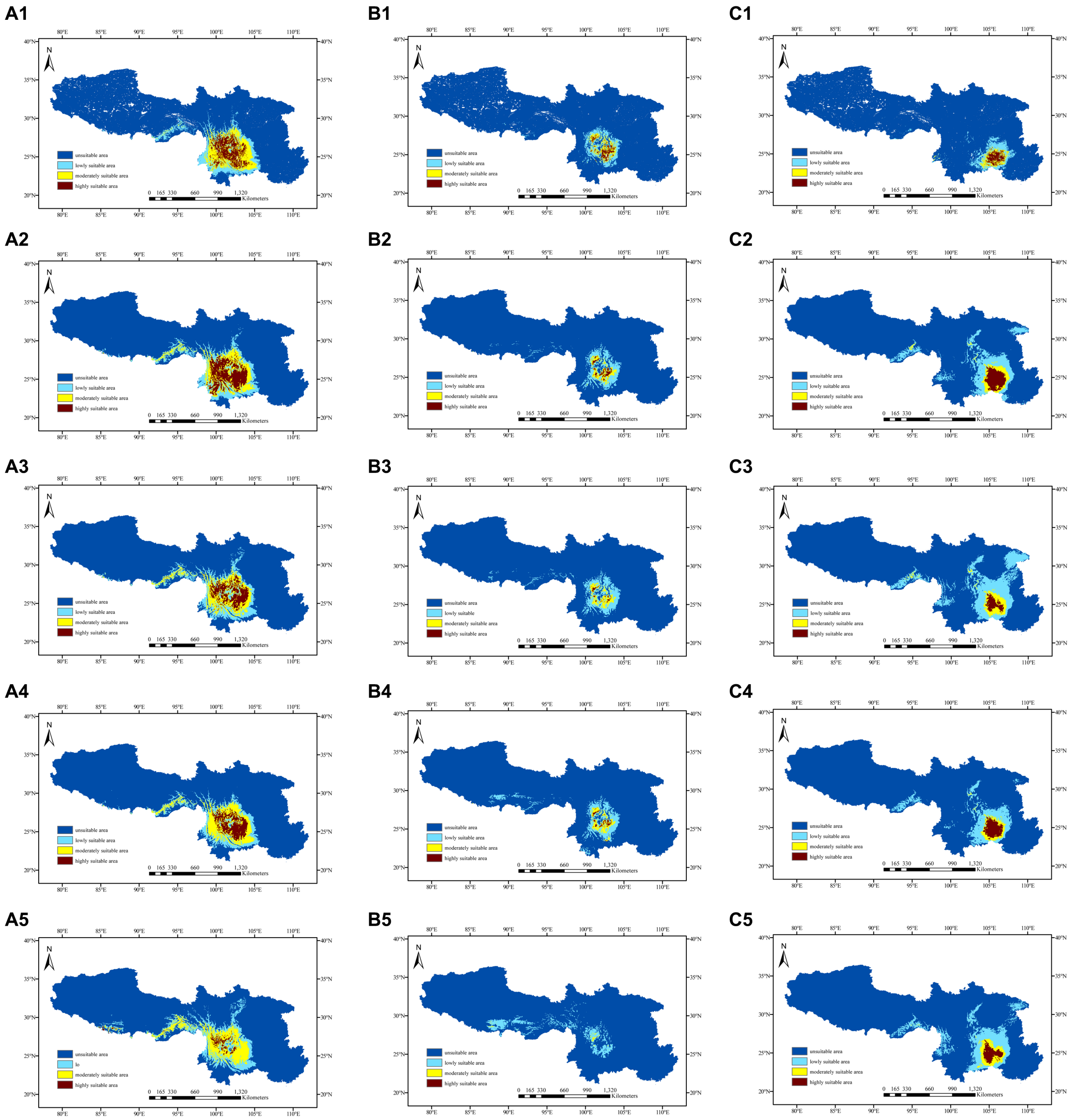

FIGURE 4
Predicted current and future potential distribution of three *P. yunnanensis* varieties under different scenarios. **(A)** var. *yunnanensis*; **(B)** var. *pygmaea*; **(C)** var. *tenuifolia*; (1) current climate; (2) future climate scenario SSP 1–2.6 in 2040–2060; (3) future climate scenario SSP 5–8.5 in 2040–2060; (4) future climate scenario SSP 1–2.6 in 2060–2080; (5) future climate scenario SSP 5–8.5 in 2060–2080.

important roles than precipitation in affecting the distribution of the three varieties of *P. yunnanensis* (Table 3), indicating that that temperature has a more pronounced impact on the distribution of *P. yunnanensis* compared to precipitation. Similar findings have been reported for other species. For instance, Wang et al. (2013) found that temperature-related variables played more crucial roles compared to precipitation factors in examining the correlation with the geographical distribution of three taxa of *Akebia Decne*. Tang et al. (2021) also found that pine species exhibit a higher degree of sensitivity toward temperature fluctuations than other environmental factors. Besides temperature, fire also played an important role in the distribution of *P. yunnanensis* varieties. Wildfire is an ancient natural phenomenon that is an important driver of species distribution and community succession in ecosystems (Magadzire et al., 2019). The central Yunnan Plateau ecosystem, where the *P. yunnanensis* is located, is a fire-dependent ecosystem (Su et al., 2015). *P. yunnanensis* is frequently exposed to forest fires and is a dominant species in such fire-prone environments. Fire-adapted traits have developed in *P. yunnanensis* and these fire-adapted traits exhibited obvious intraspecific variation (Pausas, 2015). For example, the shrubby variety *pygmea* has a higher serotiny level

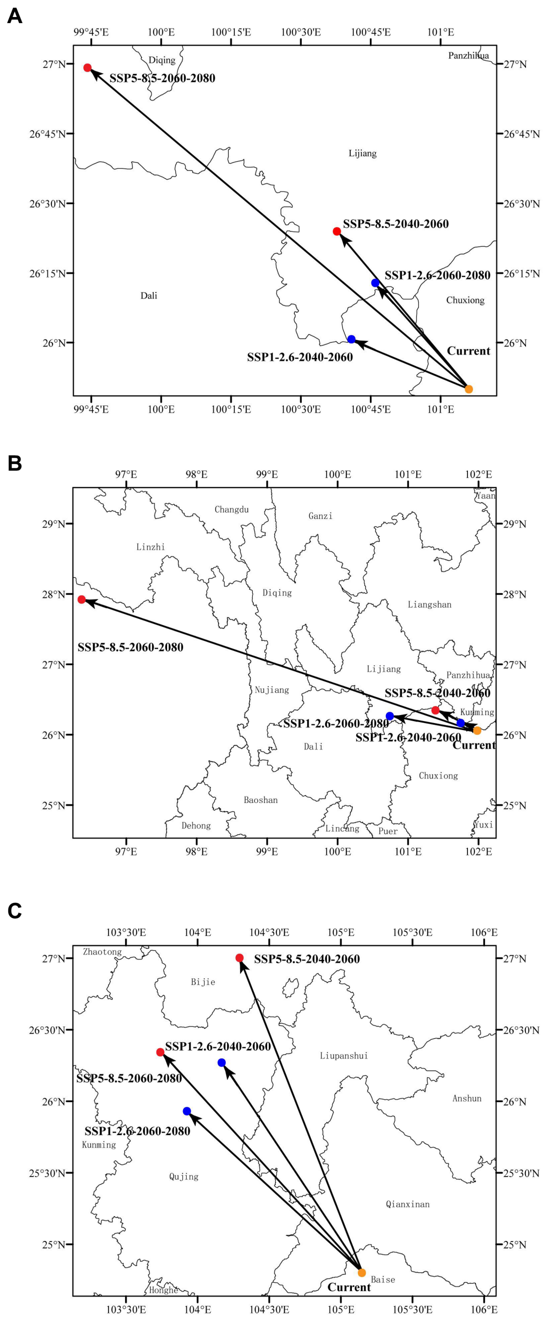

FIGURE 5
The shift of distributional centers under different climate scenario for the three *Pinus yunnanensis* varieties. **(A)** var. *yunnanensis*; **(B)** var. *pygmaea*; **(C)** var. *tenuifolia*; Arrow indicates magnitude and direction of predicted change through time.

and stronger resprouting ability than the tree-forming varieties var. *yunnanensis* and var. *tenuifolia*. Tree-forming varieties have thicker bark than the shrub-forming variety, and have self-pruning ability, which is absent in the shrub-forming variety. The intraspecific variation of fire adaptations allowed *P. yunnanensis* varieties adapted to different fire regimes. Most species distribution studies have focused on environmental factors, such as climate and soils, with little consideration of the effects of wildfire conditions on species distribution patterns. Our study proved that fire regime is a critical factor that can affect the distribution of plant species.

Climate change can lead to rearrange species distributions, as plants tend to follow their familiar climates (Madsen-Hepp et al., 2023). For var. *yunnanensis*, the probability of presence expands as temperature seasonality (Bio4) increases, while for var. *pygmaea*, the probability of presence decreases when isothermally (Bio3) increasing (Supplementary Figure S2). This discrepancy probably due to the narrower ecological niche and smaller range of temperature suitability of var. *pygmaea* compared to var. *yunnanensis*. Previous studies showed that the distribution of var. *pygmaea* is strongly affected by annual mean temperature and mean temperature of coldest quarter temperature changes (Chen et al., 2021), indicating that var. *pygmaea* needs more stable seasonal temperatures. Var. *tenuifolia* shows a gradual increase in the probability of presence with an increase in mean annual fire occurrence (MAF), indicating that var. *tenuifolia* can survive and regenerate in fire-prone environment. Var. *tenuifolia* is characterized by thick bark and tall crowns, allowing it has a significant advantage in survival surface fires and a greater competitive edge within the community (Pausas et al., 2017). As the probability of presence of var. *yunnanensis* is predicted to be expanded, which will undoubtedly be beneficial to the timber economy. However, for var. *pygmaea*, suitable areas, especially highly suitable areas, will decrease indicating that carrying out some effective protection measures are necessary for var. *pygmaea*. In future, *P. yunnanensis* varieties are likely to expand their range toward higher latitudes as temperatures rises, encompassing new habitats that are currently outside their distribution range. The predictions are consistent with the view that climate warming is driving many species to move to higher latitudes (Guo et al., 2023; Wang et al., 2023).

Ecological niche modeling has been recognized as an effective method to make predictions and control measures for species distribution patterns, but this method still has drawbacks (Li et al., 2023) (Kolanowska, 2023). For example, predicting species distribution maybe inexact when relying solely on a limited set of environmental variables and the results may vary with the environmental variables being used in the model. In this study, we considered the effects of climate, elevation, soil and fire on the distribution of the three varieties of *P. yunnanensis*. In realty, there are many other factors that can influence the distribution of species (Ramachandran et al., 2020). For example, pests, diseases, and human activities are also important factors affecting the distribution of *P. yunnanensis* (Huang et al., 2022; Liu et al., 2022). Further research is needed in order to better evaluate the factors effecting the distribution of *P. yunnanensis* and predict the dynamic in its distribution changes. The combined effects of geographic and environmental factors have created the genetic and phenotypic differentiation among *P. yunnanensis* varieties (Wang et al., 2013). In addition to climatic conditions, the distribution of species is also influenced by specific traits of the species itself (Bradie and Leung, 2017). For example, high serotiny level facilitated var. *pygmaea* to survive in wildfires (Tang et al., 2013). Therefore, how trait variations affect the distribution of *P. yunnanensis* varieties are also necessary to explore.

5 Conclusion

For this study, temperature seasonality (BIO4) emerged as the most influential factor affecting var. *yunnanensis*, isothermally (BIO3) stands out as the most critical factor for var. *pygmaea*, whereas mean annual fire occurrence (MAF) had the greatest impact on var. *tenuifolia*. Fire affected the distribution of all the three varieties, indicating that fire regime played a vital role in shaping the distribution of *P. yunnanensis* varieties. Under global warming, the suitable habitat range for the three varieties is expected to expand, and the distribution centroids for all three varieties are projected to shift toward to higher latitudes. Our study can facilitate the conservation and utilization of *P. yunnanensis* varieties. However, our study is constrained by a limited set of environmental variables. To better assess the further distribution of *P. yunnanensis* varieties, additional factors should be considered. For varieties with decreasing suitable areas, conservation measures should be implemented to protect them.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

JF: Writing – original draft. BW: Writing – review & editing. MX: Writing – review & editing. SZ: Writing – review & editing. CH: Writing – review & editing. XC: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1308416/full#supplementary-material

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