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Ecological niche shifts affect the potential invasive risk of *Phytolacca americana* (Phytolaccaceae) in China

Yifeng Xu[1†], Xingzhuang Ye[1†], Qianyue Yang[1], Huiying Weng[1], Yipeng Liu[1], Sagheer Ahmad[2], Guofang Zhang[1], Qiuliang Huang[1], Tianyu Zhang[3] and Bao Liu[1*]

Abstract

Background: Predicting the potential habitat of *Phytolacca americana,* a high-risk invasive species, can help provide a scientific basis for its quarantine and control strategies. Using the optimized MaxEnt model, we applied the latest climate data, CMIP6, to predict the distribution of potential risk zones and their change patterns for *P. americana* under current and future (SSP126, SSP245, SSP585) climate conditions, followed by invasion potential analysis.

Results: The predictions of MaxEnt model based on R language optimization were highly accurate. A significantly high area of 0.8703 was observed for working characteristic curve (AUC value) of subject and the kappa value was 0.8074. Under the current climate conditions, the risk zones for *P. americana* were mainly distributed in Sichuan, Chongqing, Guizhou, Hunan, and Guangxi provinces. The contribution rate of each climatic factor of *P. americana* was calculated using the jackknife test. The four factors with the highest contribution rate included minimum temperature of coldest month (bio6, 51.4%), the monthly mean diurnal temperature difference (bio2, 27.9%), precipitation of the driest quarter (bio17, 4.9%), and the warmest seasonal precipitation (bio12, 4.3%).

Conclusion: Under future climatic conditions, the change in the habitat pattern of *P. americana* generally showed a migration toward the Yangtze River Delta region and the southeastern coastal region of China. This migration exhibited an expansion trend, highlighting the strong future invasiveness of the species. Based on the predictions, targeted prevention and control strategies for areas with significant changes in *P. americana* were developed. Therefore, this study emphasizes the need of an integrated approach to effectively prevent the further spread of invasive plants.

Keywords: *Phytolacca americana*, MaxEnt, Invasive plants, Climate change

Background

Invasive alien plants affect ecosystem stability in various ways, such as reduced biodiversity of native plants (Weidlich et al. 2020). Biodiversity loss negatively affects the ability of ecological communities to obtain biologically essential resources, such as carbon and nitrogen. Moreover, the renewability and decomposition efficiency of these resources is also reduced. Increasing loss can reduce the rate of ecosystem recovery, ultimately leading to irreversible consequences (Cardinale et al. 2012). The IPCC (Intergovernmental Panel on Climate Change) Sixth Assessment Report Working Group II indicates that climate change has had more negative impacts than predicted, resulting in excessive carbon emissions due to global warming (Tollefson 2022). Recent studies have shown that biological conservation can significantly reduce the impacts of climate change (Shin et al. 2022). As climate anomalies influence species distributions, detecting the response of invasive species to climate

†Yifeng Xu and Xingzhuang Ye contributed equally to this work

*Correspondence: fafulb@163.com

[1] Forestry College, Fujian Agriculture and Forestry University, Fuzhou 350002, Fujian, China
Full list of author information is available at the end of the article

change can assist in developing strategies to mitigate the damage they cause (Zhang et al. 2014). To avoid the expansion of invasive species and the collapse of native ecological communities worldwide, strict measures shall be adopted globally to reduce GHG emissions (Mungi et al. 2018). Therefore, it is crucial to understand the trends in the spread of invasive species under climate change to prevent and control invasions in a rational and effective manner.

Ecological niche models (ENMs) are used to combine occurrence data with environmental data to create correlations to understand the ecological needs of species and predict their habitat suitability (Phillips et al. 2017). A widespread tool for modeling species distributions and environmental-ecological niches is the MaxEnt model, which can simulate the geographic distribution of species suitable for survival more accurately than ENMs (Elith et al. 2011). It is a crucial component of various applied studies on species ecology and conservation (Ye et al. 2022). The MaxEnt model provides a conservative and effective prediction of invasive species management areas (Amanda et al. 2016). This model has shown remarkable performance in predicting the potential habitats of endangered plants and animals (Ye et al. 2022), pest and disease control (Hosni et al. 2022), and species invasion (Siller-Clavel et al. 2022). The data used in this study are the shared socioeconomic pathways (SSPs) under the BCC-CSM2MR (Beijing Climate Center-Climate System Model-Medium Resolution), of which SSP126, SSP245, and SSP585 are the representatives.

Phytolacca americana, native to North America, is a perennial herb in the family Phytolaccaceae. It was artificially introduced in China as a medicinal plant. Since its discovery in 1935 in Hangzhou, Zhejiang Province, this species has undergone a population establishment phase and a dispersal phase, spreading to most of the provinces in China after 1960. However, it is still in the dispersal phase at present (Wang et al. 2021). It is commonly found in grasslands, forest margins, roadsides, or shrublands. After a long period of adaptation, it has become more invasive, affecting the ecology of some areas and damaging the growth and development of other plants. The whole plant is toxic, containing toxins such as phytolaccatoxin, pokeweed saponin, and phytolaccine. Its rhizome is similar to ginseng, for which it is easily mistaken, and humans consume it and develop headache, vomiting, nausea, diarrhea, and in severe cases, heart paralysis, coma, and even death (Ma et al. 2014). However, its roots are used to treat edema, rheumatism, and emmenagogue. Though valuable for its medicinal qualities, its unique fruiting and spatial heterogeneity adversely affect the ecology of sandy coastal protected forests in China, resulting in a significant loss of socioeconomic resources. Its seeds are often dispersed by fruit-eating animals, especially birds, accelerating its invasion to natural ecosystems (Fu 2012; Xiao et al. 2022). *P. americana* has been listed in the fourth batch of invasive alien species by the Ministry of Ecology and Environment in China. Its tolerance against low light conditions and reproductive capacity are far better than that of the native species (Liu et al. 2022). Chen et al. (2021) utilized CMIP5 data to predict the potential geographic distribution of *P. americana*; however, this study mainly focused on the delineation of cultivated habitats. Is the current extent of the risk zone under the latest data consistent with previous predictions? How will the distribution pattern of *P. americana* change as a result of future climate change? What are the main climatic factors limiting the geographical distribution of *P. americana*? How do these factors affect geographic distribution? These questions remain unresolved and continue to constrain the ecology of controlling *P. americana*.

The purpose of this study is to optimize the MaxEnt model using the ENMeval package in R language to simulate the distribution of potential habitats of *P. americana* in China for current and future periods (2041–2060, 2081–2100) using the Shared Socioeconomic Pathway (SSP126, SSP245, and SSP585) from the 6th International Coupled Model Intercomparison Project (CMIP6). Moreover, CMIP6 data are derived from CMIP5 projections of future emissions of greenhouse gases under various climate policies. CMIP6 considers not only the relationship between CO_2 and climate, but also makes climate change projections more accurate under the double reduction policy (Zhu et al. 2021). Using China as the study area to provide a scientific reference and theoretical basis for the control of *P. americana* and selecting 19 relevant climatic factors, we investigate the distribution of potential risk zones, the spatial variation patterns, and the shift in the mass center of risk zones.

Methods

Data preparation

The data relating to the distribution points of *P. americana* were obtained from literature records and searches of the Chinese Digital Herbarium (http://www.cvh.org.cn/) and the Global Biodiversity Information Facility (https://www.gbif.org/). The data were based on latitude and longitude queries (https://map.jiqrxx.com/jingweidu/). A total of 427 data points were collected on the spatial distribution of *P. americana* in China, including all the known natural distribution areas of *P. americana* in China. After filtering the distribution points, to reduce the overfitting caused by the cluster effect, the points were imported into ArcGIS in CSV format. CGCS2000 3Degree GK Zone 35 was selected as the projection coordinate system to perform a 10 km diameter buffer zone analysis to ensure that duplicate sample points within a 10 km range were removed until only one point remained. In total, 405 valid spatial distribution data were obtained for *P. americana*.

We studied the shared economy pathways identified by CMIP6. The pathways were derived from the World Climate Database (WorldClim 2.1, http://worldclim.org). Using the 1:14 million map vector of China as the base map for hiding the 19 bioclimatic factors, the 19 bioclimatic factors were extracted for 2050s (2041–2059) and 2090s (2081–2099) using the current and SSP126, SSP245 and SSP585 scenarios (all at a resolution of 2.5 arc-minute). Using a 1:14 million vector map of China as a base map, the mask yielded the 19 climate factors required for this study. The point interpolated data were analyzed with Pearson correlation analysis in SPSS 2.2. When the correlation between two environmental factors is greater than or equal to 0.8, only one of the factors is selected (Ranjitkar et al. 2014). Ultimately, nine bioclimatic factors were selected for modeling (Ye et al. 2020), including the mean diurnal range (bio2), isothermally (bio3), maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), mean temperature of the wettest quarter (bio8), annual precipitation (bio12), precipitation seasonality (bio15), precipitation of the driest quarter (bio17), and precipitation of the warmest quarter (bio18).

MaxEnt modeling and validation

Two parameters, the regularization multiplier (RM) and feature combination (FC), were optimized using the ENMeval package in R language. The regularization multiplier was set to 0.54, in 0.5 increments, for a total of 8 regulation multipliers. Eight feature combinations (L, LQ, H, LQH, LQHP, LQHPT, HPT, and QPT) were used, where L is linear, Q is quadratic, H is hinge, P is product, and T is threshold. A combination of 64 parameters was tested, and the combination was tested again for its suitability to the species distribution points based on the Akaike information criterion (AICc). The difference between the training AUC and test AUC values (AUC.DIFF), and the delta AICc in the result file was used to evaluate the complexity and fitting degree of different parameter combinations (Burnham and Anderson 2004). A combination of model parameters at the lowest AICc value (delta.AICc = 0) was adopted for MaxEnt modeling (Phillips et al. 2017).

The CSV file containing the latitude and longitude of 405 distribution points of *P. americana* with the 9 selected climate factors was imported into MaxEnt, the jackknife test was used to determine the weights of each variable, and the response curves for each of the environmental variables were generated. We randomly selected 75% of the distribution point data as the training data, 25% was used as the test data, and the remaining variables were left unchanged. Moreover, the accuracy of the AUC value of the receiver operating characteristic curve (ROC) and AUC value, with the repeat run type set to Bootstrap and the output format set to logistic, was calculated 10 times. Kappa and true skill statistics (TSS) were used to measure MaxEnt's prediction accuracy. The ASCII file of the output mean was reclassified using ArcGIS, and the riskiness of 0.6 to 1 was classified as highly risky zone, 0.5 to 0.6 as moderate risk zone, 0.2 to 0.5 as poor risk zone, and 0 to 0.2 as risk-free area. The area of each risk zone was calculated using a manual grading method. The predicted AUC value of 0.6 was considered poor, the average value ranged from 0.7 to 0.8, of the good AUC value was 0.8 to 0.9 and the excellent value was 0.9 to 1.0. The criteria for Kappa and TSS values were: excellent, 0.85 to 1; very good, 0.7 to 0.85; good, 0.55 to 0.7; fair, 0.4 to 0.55; and fail, less than 0.4 (Ye et al. 2022; Allouche et al. 2006).

Spatial distribution patterns and habitat distribution centroid changes

The areas with a probability of distribution greater than 0.5 were assigned a value of "1" for areas with high and moderate habitability and "0" for areas with low and very low habitability. Based on the potential habitat area of modern species, different types of habitat area changes were defined according to the changes in the matrix (0, 1): the increased area ($0 \rightarrow 1$), the unsuitable area ($0 \rightarrow 0$), the lost area ($1 \rightarrow 0$) and the reserved area ($1 \rightarrow 1$). At last, the matrix change values were imported into ArcGIS and the area of each change zone was calculated (Ye et al. 2022).

Specifically, areas with risk factor greater than or equal to 0.5 were considered risk zones. ArcGIS was used to identify seven climate zones, including current, 2050s-SSP126, 2050s-SSP245, 2050s-SSP585, 2090s-SSP126, 2090s-SSP245 and 2090s-SSP585. The centroids of risk zone were transformed into vector particles using ArcGIS, which reflected spatial changes in risk zone in both magnitude and direction. The centroid in the risk zone under a given set of conditions was compared with the changes in the centroid under different climatic conditions in each period, and the distance of the centroid shift was calculated.

Results

Evaluation of model optimization results and accuracy

For the MaxEnt model, the default settings were: RM = 1, FC = LQHPT, delta.AICc = NA, and RM = 1. The optimized delta.AICc and avg.diff.AUC values were both

Table 1 Importance of various environmental parameters on the distribution of *P. americana*

Environmental variables	PC	PI (%)	TRGw	TRGo	TG_w	TGo	AUCw	AUCo
Bio6	51.41	34.02	1.3525	1.1673	1.2950	1.1516	0.8960	0.8683
Bio2	27.91	16.78	1.3648	1.1694	1.3109	1.1424	0.8983	0.8724
Bio17	4.91	11.60	1.3629	1.1001	1.3255	1.0680	0.8978	0.8668
Bio12	4.29	6.17	1.3728	1.1097	1.3214	1.0936	0.8988	0.8659
Bio18	3.23	7.69	1.3671	1.0037	1.3175	0.9954	0.8976	0.8576
Bio5	2.98	10.78	1.3585	0.5011	1.2938	0.5055	0.8946	0.7675
Bio3	2.32	3.59	1.3737	0.2055	1.3242	0.2078	0.8989	0.6672
Bio15	2.02	6.76	1.3710	0.6277	1.3144	0.6127	0.8980	0.7951
Bio8	0.93	2.61	1.3731	0.4272	1.3169	0.4279	0.8974	0.7350

PC is percent contribution; PI is permutation importance; TRG_O is the regularization training gain using the factor alone; TRG_W is the regularization training gain using other factors; TG_O is the test gain using the factor alone; TGw is the test gain using other factors; AUCw is the area under the receiver operating characteristic curve using other factors; AUCo is the area under the working characteristic curve of the subjects using the variable alone

lower than the default settings. At the optimal parameter setting, the AUC value of the current fitness zone distribution predicted by the model simulation was 0.8703, and the AUC value of the potential risk zone for each period was > 0.8, indicating that the model predicted good results. A kappa value of 0.8074 and TSS value of 0.8171 indicated that the predicted outcome was very good.

Climatic factors limiting the pattern of modern potential ranges

In Table 1, the four most important factors cumulatively contributed 88.5%, including the minimum temperature of the coldest month (bio6, 51.4%), mean diurnal range (bio2, 27.9%), precipitation of the driest quarter (bio17, 4.9%) and annual precipitation (bio12, 4.3%). The permutation importance was 73.2% for four most important factors, including the minimum temperature of the coldest month (bio6, 34%), mean diurnal range (bio2, 16.8%), precipitation of the driest quarter (bio17, 11.6%), and the maximum temperature of the warmest month (bio5, 10.8%). When using only one variable in the jackknife test, the minimum temperature of the coldest month (bio6), mean diurnal range (bio2), precipitation of the driest quarter (bio17), and annual precipitation (bio12) had the highest training gain, test gain, and AUC values. Accordingly, the minimum temperature of the coldest month (bio6), mean diurnal range (bio2), precipitation of the driest quarter (bio17), and annual precipitation (bio12) were the main factors influencing the distribution of the potential habitat of *P. americana*. By comparing the four factors, it can be seen that the minimum temperature of the coldest month (bio6) and the mean diurnal range (bio2) were the most critical factors (Table 1).

Based on the probability of existence > 0.5 as a criterion, the range of minimum temperature of the coldest month (bio6) was − 2 to 9 °C, with 5.8 °C as the optimum temperature. The range of the mean diurnal range (bio2) was from 2.6 °C to 8.3 °C, with 5.7 °C being the optimum value. The suitable range for precipitation of the driest quarter (bio17) was from 50 to 650 mm, with the optimum value being 580 mm. The suitable range for annual precipitation (bio12) was from 970 to 1900 mm, with an optimum value of 1500 mm (Fig. 1).

Under current climatic conditions, MaxEnt simulations indicate that suitable areas for pendulous *P. americana* can be found in all regions except Xinjiang, Qinghai, Inner Mongolia, Ningxia, Jilin, and Heilongjiang. These regions have an area of 227.90×10^4 km^2, accounting for 23.71% of the national area. The moderately suitable area includes mostly south-central Jiangsu, Zhejiang, most of Fujian, northern Guangdong, northern Guangxi, southern Anhui, most of Jiangxi, Hubei, Hunan, Guizhou, Chongqing, southeast Sichuan, and north Taiwan. These regions cover an area of 73.14×10^4 km^2, accounting for 7.61% of the national area. The high risk zones are mainly concentrated in Sichuan, Guizhou, Guangxi, Hunan, and northern Taiwan, with patchy distribution near the junction of Sichuan and Guizhou, southern Hunan, and sporadic distribution in Chongqing, Hubei, Fujian, Zhejiang, Guangdong, Anhui, and Jiangxi. The area coverage is 12.13×10^4 km^2, which makes 1.26% of the total area.

By comparing the results of the current climate scenarios with the three future climate scenarios (SSP126, SSP245, and SSP585), it is evident that the area of the potential risk zone of *P. americana* is gradually increasing. Under the SSP126 emission scenario, the high risk zones in the 2050s will shrink by 15.85% compared to the current scenario, primarily due to reduction in the high risk zone in Sichuan. The high risk zones in the 2090s, on the other hand, will increase by 19.17%, possibly due to transformation of the most moderate risk zones in northern Fujian and Guangxi into high risk zones. Therefore,

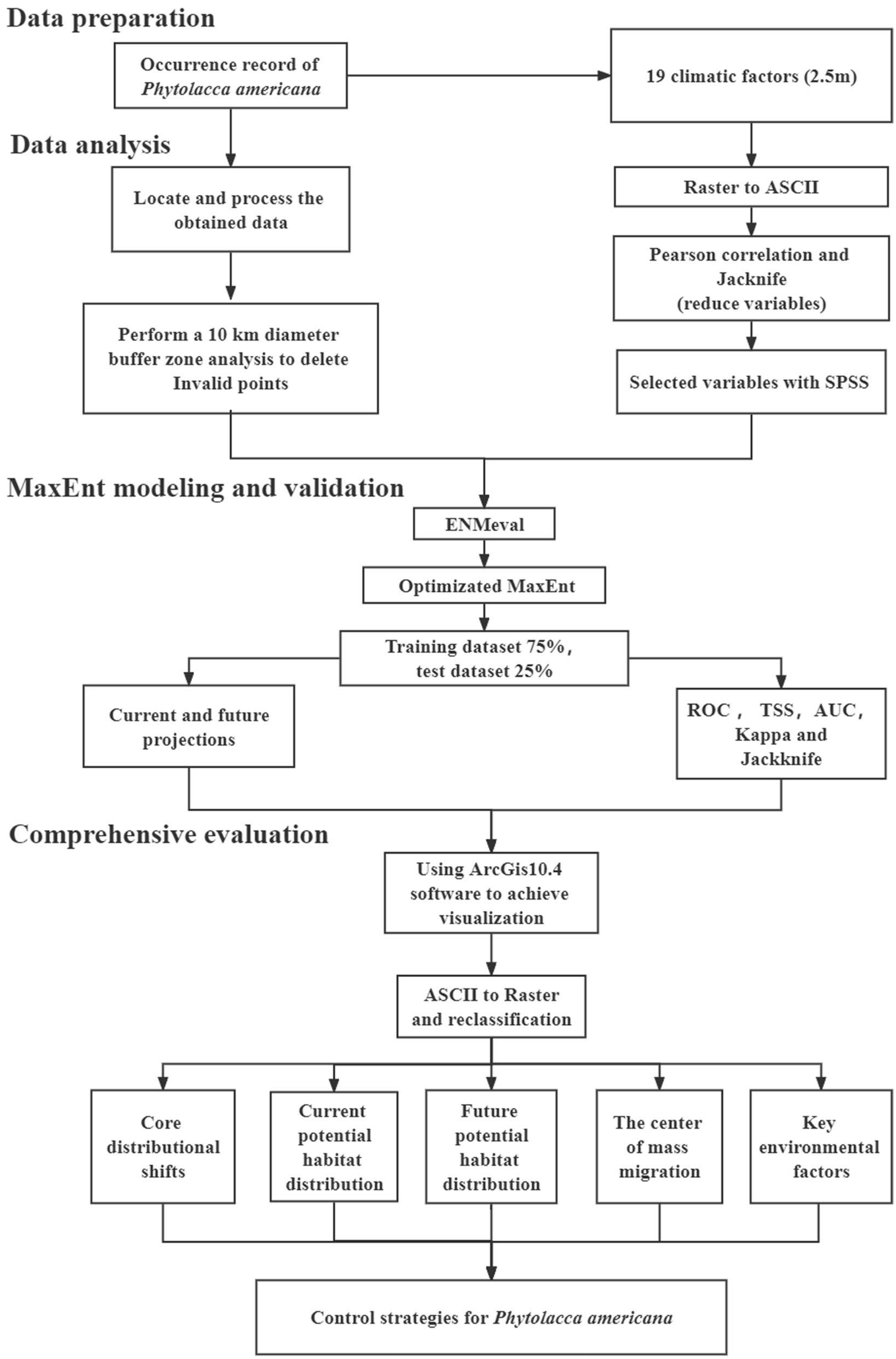

Fig. 1 Study flow diagram for processing

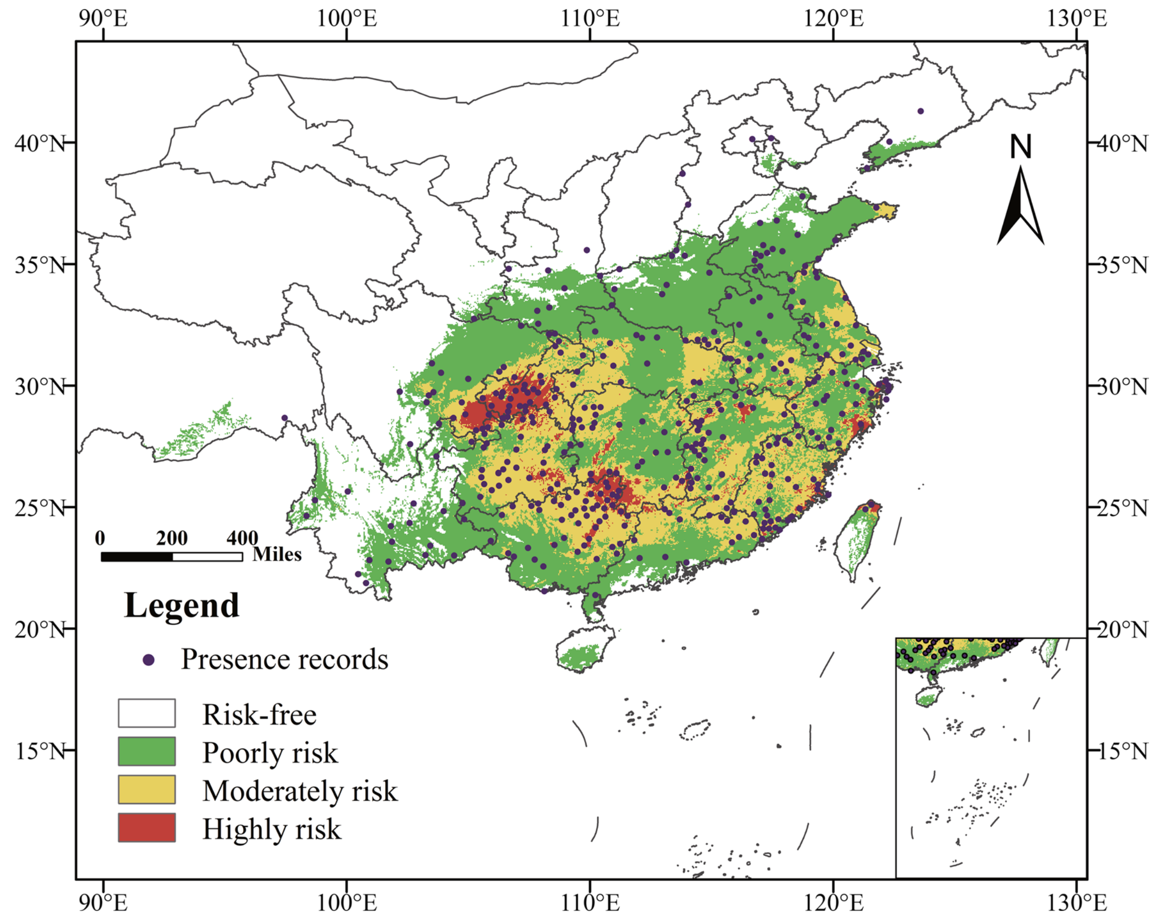

Fig. 2 Current habitat suitability distribution of *P. americana*

the moderate risk zones are decreased by 28.89%, while the poor risk zones are increased by 11.69%. Under the SSP245 emission scenario, the change in the area of the risk zone in the 2050s is less noticeable, but the total area still increases The change in the area of the risk zone in the 2090s is substantial, predominantly influenced by changes in the areas of high- and medium-risk zones. The area of the high-risk zone increases by 14.79%, while the area of the medium-risk zone decreases by 16.19%. As with SSP585, the overall trend is similar, with Shanghai becoming a high risk zone. Considering the SSP585 emission scenario, the 2050s and 2090s increase by 10.02×10^4 km^2 and 5.92×10^4 km^2, respectively, suggesting that the spread of potential risk zones for *P. americana* may be advantageous under the high concentration emission scenario. The 2050s-SSP585 scenario is particularly significant, with the largest increase in total risk zone compared to present times, up to 10.02×10^4 km^2. In Fig. 2, the high risk zones in Sichuan and Guizhou gradually decrease in size and are concentrated in the eastern coastal areas (Table 2).

Changes in the spatial pattern of habitats

Based on the current potential risk zone for *P. americana*, with the exception of 2090s-SSP126 and 2090s-SSP245, the increase in area was greater than the loss of area, indicating an expansion trend in in a short time. In the 2050s-SSP585 period, the largest rate of growth was 32.52%, and the areas of increase were mainly located in southeastern Sichuan, central Hunan, central Guangdong, Zhejiang, Jiangsu, and Shanghai. In comparison, the greatest loss rate was 19.10%, and the overall rate of change was 13.42%. The increasing rates in the 2050s-SSP126 and 2050s-SSP245 periods were 27.17% and 26.99%, respectively, which were lower than the increasing rates in the 2050s-SSP585 period. The overall rate changes during the 2050s-SSP126 and 2050s-SSP245 were only 1.76% and 2.12%, respectively, substantially lower than the rate changes in the 2050s-SSP585 period. The increasing rates during 2090s-SSP126, 2090s-SSP245, and 2090s-SSP585 periods were 19.12%, 23.08%, and 27.36%, respectively. In fact, the loss rate was even more evident for the three different emission concentrations of 2090s, including

Table 2 Changes of potential risk zones of *P. americana* in different periods (unit: × 10^4 km^2)

Type of risk zone	Current	2050s-SSP126	2050s-SSP245	2050s-SSP585	2090s-SSP126	2090s-SSP245	2090s-SSP585
Low risk zone	142.63	148.41	141.27	141.28	161.50	154.07	147.00
Moderate risk zone	73.14	76.65	75.73	85.00	56.75	62.94	73.62
High risk zone	12.13	10.47	11.71	11.63	15.01	14.23	13.20
Total risk zone	227.90	235.53	228.71	237.91	233.26	231.24	233.82

2050s. 2041–2060; 2090s. 2081–2100; SSP126. Sustainable development pathway; SSP245. Sustainable intermediate development pathway; SSP585. Fossil fuel-based development pathway

SSP126 (35.08%), SSP245 (32.46%), and SSP585 (25.47%). Therefore, considering the concentrated emissions, it can be concluded that higher the concentration, greater is the rate of increase. Compared to the other future climate conditions, the retention rate for the 2050s-SSP585 period was as high as 80.54%, which was greater than the retention rate for all other future climate conditions. In the six periods, southern Chongqing, northern Guangxi, central Guizhou, south Hunan, southeastern Fujian, and eastern Zhejiang were always retained, whereas Hubei, Sichuan, Guangdong, Jiangxi, Shandong Peninsula, and northern Taiwan were more variable (Table 3).

The migration trends of core habitat distributions of *P. americana*

Under modern climatic conditions, the center of mass of the *P. americana* risk zone is located in Xiangxiang city in Hunan Province (27°46′38.74″, 112°29′24.97″). Under SSP126, the center of mass for the 2050s is located in Xiangxiang city, Hunan Province (27°53′47.59", 112°22′42.42"), which is shifted 17.20 km to the northwest of the current period center of mass. The center of mass for the 2090s is located in Xiangtan County, Hunan Province (27°31′47.69″, 112°55′13.86″), which is shifted 67.11 km to the southeast of the 2050s center of mass. Under SSP245, the center of mass for the 2050s is situated in Yuelu District, Hunan Province (28°1′0.23″, 112°52′45.61″), which is 46.55 km to the northeast of the current period center of mass. The center of mass for the 2090s is located in Yutang District, Hunan Province (27°49′0.40″, 112°59′32.334). Under SSP585, the center of mass for the 2050s is located in Xiangtan County, Hunan Province (27°45′21.97″, 112°54′1.26″), which is 17.20 km to the southeast of the current period center of mass. The mass center for the 2090s is positioned in Xiangtan County, Hunan Province (27°33′0.12″, 112°51′45.98″) and it is 17.20 km to the southeast of the current period center of mass. For the 2090s, the mass center is sited in Xiangtan County, Hunan Province (27°33′0.12″, 112°51′45.98″), with a shift of 23.19 km to the west-southwest of the 2050s center of mass (Figs. 3, 4, 5).

Discussion

Potential geographical distribution

Based on the MaxEnt ecological niche model and the selected distribution points, the model was combined with ArcGIS and optimized using R language to predict the potential distribution of *P. americana* in China under current and future climatic conditions. The predicted AUC values for all future periods were > 0.9, indicating excellent predictions.

Based on the MaxEnt model, the results indicate that *P. americana* is concentrated in the area south of the Qinling and Huaihe Rivers, which is consistent with the species' current distribution (Wu et al. 2003). This species was first discovered in Hangzhou, Zhejiang Province, and was found suitable for growth in the provinces along the Yangtze River (Wang 2006). The suitability area simulation in this study also covers this region, indicating the accuracy of the model.

The future potential habitat of *P. americana* in China under the six different scenarios follows a similar trend, shifting from Chongqing, Sichuan, and Guangxi to the southeast coast of China, with the SSP126 scenario being the least pronounced. In contrast, the 2050s-SSP585 scenario forecasts the largest total habitat area of 237.91×10^4 km^2, accounting for 24.74% of the area in China. The prediction is presumably based on the finding that an increase in CO_2 concentration results in increased root biomass in *P. americana* (Zhang et al. 2010). The shift from low to high and moderate habitats in Fujian under the 2090s-SSP126 scenario is different from that in the other scenarios and may be related to the tendency of *P. americana* to encroach upon hilly areas (Zima and Štefanić 2021). According to some studies, the SSP126 emission scenario is in line with China's carbon-neutral target (Zhou et al. 2022), which is important to strengthen the prevention and control of *P. americana* in Fujian and the entire country in advance under the premise of a dual carbon policy.

Climatic factors constraining modern geographical distribution

Climate warming may reduce the efficiency of biological control and promote invasions of *P. americana*, suggesting the importance of interactions between ecological

Table 3 Changes of the spatial pattern area of *P. americana* in different periods

Period	Area (× 10^4 km^2)				Change (%)			
	Increase	Reserved	Lost	Change	Increase rate	Reserved rate	Lost rate	Change rate
2050s-SSP126	23.27	63.61	21.77	1.51	27.17	74.25	25.41	1.76
2050s-SSP245	23.12	64.36	21.30	1.82	26.99	75.13	24.87	2.12
2050s-SSP585	27.85	68.99	16.36	11.49	32.52	80.54	19.10	13.42
2090s-SSP126	16.38	55.29	30.05	− 13.67	19.12	64.54	35.08	− 15.96
2090s-SSP245	19.77	57.55	27.81	− 8.04	23.08	67.18	32.46	− 9.39
2090s-SSP585	23.44	63.37	21.82	1.62	27.36	73.98	25.47	1.89

and evolutionary processes (Sun et al. 2022). Among the climatic factors, temperature and precipitation play an essential role in determining the distribution of *P. americana*. The minimum temperature of the coldest month (bio6) and the mean diurnal range (bio2), two topmost contributors, accounted for 51.4% and 27.9% of the total contribution, respectively, indicating that the temperature is a dominant factor. The minimum temperature of the coldest month is an essential factor influencing invasive plant distribution (Zhao et al. 2022). The phenological period of *P. americana* is closely related to temperature. When the average decadal temperature drops below 10 °C, the aboveground parts die (Zhou et al. 2004), thus presumably limiting the spread of *P. americana* into the provinces north of the Yellow River, where temperature drops significantly during the coldest months (bio6). Increase in CO_2 concentration and high night temperatures (mean diurnal range) may have a neutral or positive effect on the population growth of *P. americana* in the near future (Wolfe-Bellin et al. 2006). Moreover, daily temperature variations may play an essential role in determining plant responses to warming temperatures (He et al. 2005a, b). Therefore, temperature is the dominant factor responsible for the change in the distribution of *P. americana*. The precipitation of the driest quarter (bio17, 4.9%) and the annual precipitation (bio12, 4.3%) were the the third and fourth most important contributors, respectively. Researchers found that the water uptake rate of *P. americana* seeds was positively correlated with the rate of germination and the timing of rainfall significantly affected the intensity of rain received by *P. americana* seeds (Zhai et al. 2010). The precipitation factor was shown to be an essential factor in determining the distribution density of invasive alien species (Zhou et al. 2021). *P. americana* is the best suited to the monsoonal region of China, and studies have shown that climatic conditions are conducive to the growth of *P. americana* during the same period of rain and heat (Wu et al. 2019). The temperate continental climate, with a high diurnal temperature variation, low mean temperature in the coldest month, and low rainfall and dryness, limit the normal growth of *P. americana*.

Changing patterns in the potential habitat

The increase in emission concentrations is favorable to the expansion of the potential habitat of *P. americana*. The distribution trend of *P. americana* showed an expansion trend in a short term under six future climate conditions, with the exception of 2090s-SSP126 and 2090s-SSP245. The analyses of the three scenarios showed a significant reduction in the overall distribution of 2090s-SSP126. This indicates that under the SSP126 scenario, the expansion of *P. americana* was suppressed, and the distribution of the risk zone in eastern Sichuan, northwestern Hunan, and the majority of Jiangxi was reduced. However, an expansion trend was observed in Fujian, Guangxi, Sichuan, Hunan, Jiangsu, and Zhejiang provinces. The area of *P. americana* expansion in Fujian Province encompasses nearly the whole province. Therefore, under the sustainable development scenario, there is a decline in *P. americana*, which can be maintained by strengthening the invasion prevention and control measures in Fujian, Guangxi, Sichuan, Hunan, Jiangsu, and Zhejiang provinces. The increase in emission concentration up to 13.42% in the risk zone under 2050s-SSP585 and a relative improvement under 2090s-SSP585 was favorable to the growth and development of *P. americana*. This may also demonstrate the difficulty of controlling the widespread distribution of *P. americana* under a fossil fuel-based development pathway. The Yangtze River Delta region showed the greatest expansion of habitat potential under six different climatic conditions, presumably because of the global warming due to economic prosperity and high population movement in the Yangtze River Delta region, providing favorable temperature for *P. americana* (Pyšek et al. 2020; Wang et al. 2021). However, we did not find a suitable human factor that could correctly respond to such changes. It is only a speculation and can be verified by adding anthropogenic factors in the future. No significant changes were observed in

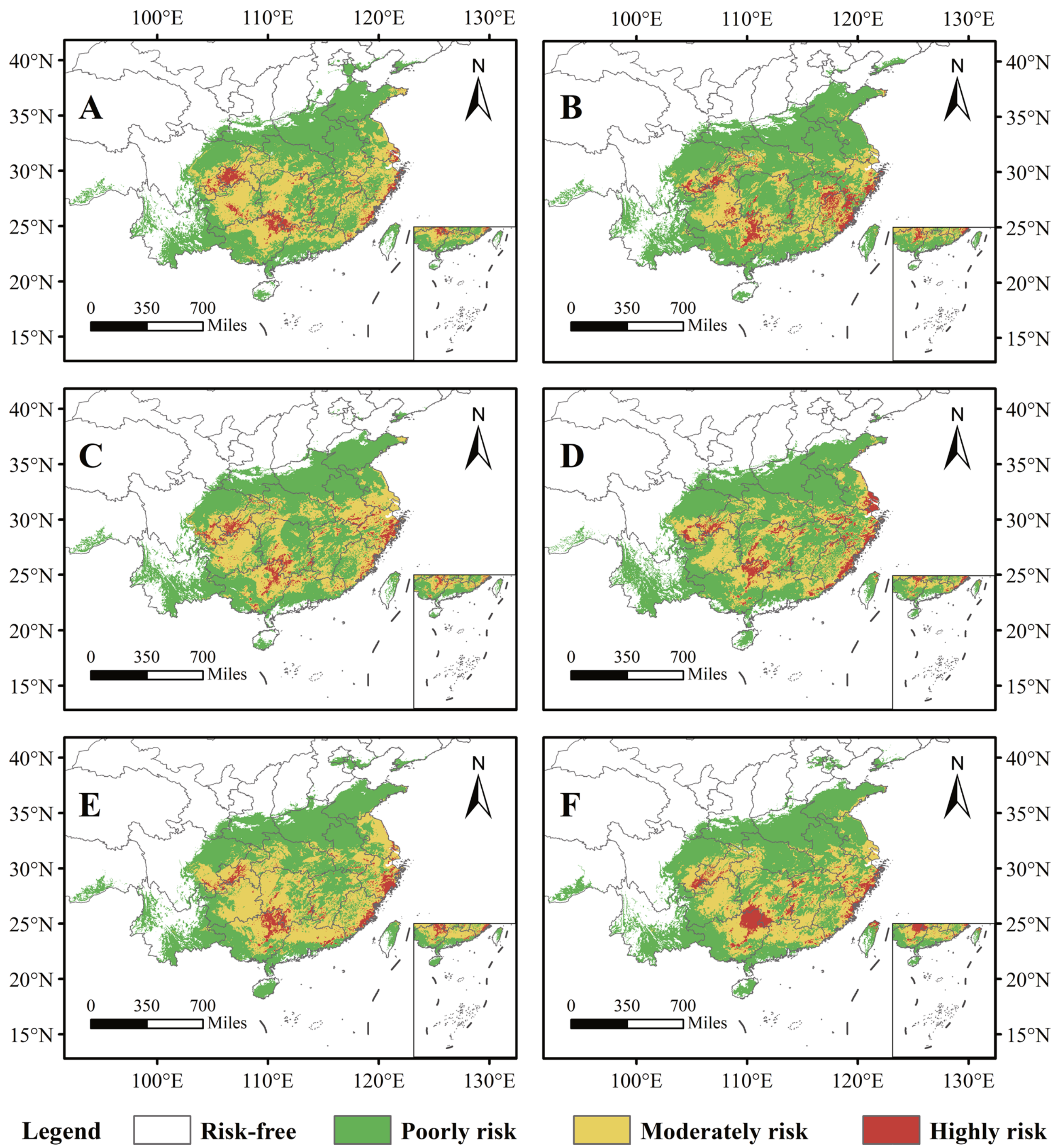

Fig. 3 Future habitat suitability distribution of *P. americana*. **a** 2050s-SSP126, **b** 2090s-SSP126, **c** 2050s-SSP245, **d** 2090s-SSP245, **e** 2050s-SSP585, **f** 2090s-SSP585

the potential habitat areas in eastern Sichuan, southern Chongqing, the lower latitudes, and the southeast coast. With the exception of SSP245, the risk zone tends to migrate southeast in both models, while the SSP245 scenario migrates first northeast and then south; hence, *P. americana* as a whole tends to migrate southeast.

Prevention and treatment strategies

Under current conditions, MaxEnt simulations suggest that the potential habitat of *P. americana* accounts for 23.71% of the national territory and has a high probability of expansion in the future, making invasion a possible threat. Among the most important drivers of species

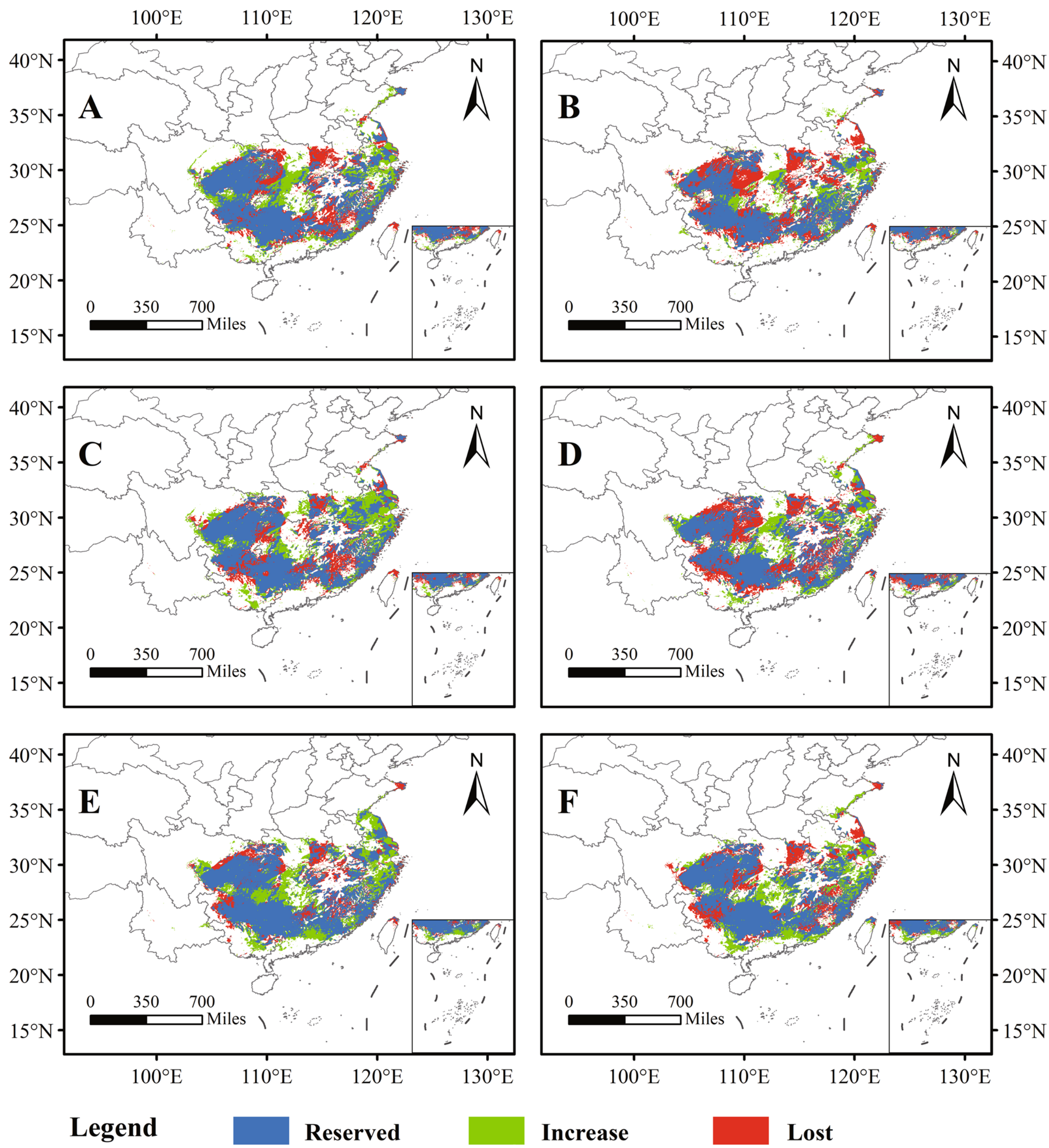

Fig. 4 Spatial pattern changes of risk zones of *P. americana* under different scenarios. **a** 2050s-SSP126, **b** 2090s-SSP126, **c** 2050s-SSP245, **d** 2090s-SSP245, **e** 2050s-SSP585, **f** 2090s-SSP585

extinction and ecosystem degradation are the invasive alien species. Invasions of biological origin are managed to maintain biodiversity, protect productive sectors such as agriculture, forestry, and fisheries, and maintain human health and well-being (Vilà and Hulme 2017). In light of the simulation results and the characteristics of *P. americana*, we can propose some recommendations to effectively control this species.

Roots of *P. americana* contain allelochemicals that can contribute to the spread of invasive species. For this

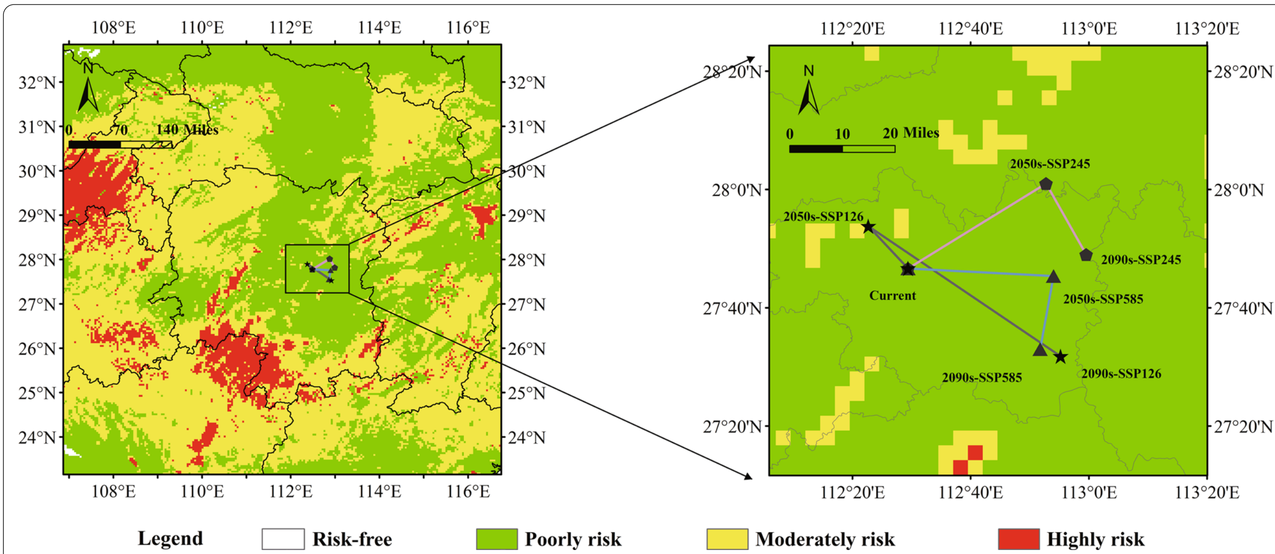

Fig. 5 The migration of the centroid of the risk zones for *P. americana*

reason, we can cut *P. americana* roots continuously to ensure complete physical control (Fu et al. 2012). Developing invasive plant eradication plans involves considering environmental factors, phenological periods, and specific techniques for their removal (Prasad et al. 2018). Moreover, the size of *P. americana* seeds influences their competitive nature, while future climate conditions may alter the quality of seeds and the reproductive behavior of plants (He et al. 2005a, b). The high number of branches and saponin content of fruits at high latitudes may also be related to plasticity, and resource allocation of *P. americana*. This information can be to devise effective control measures depending on the characteristics of the invasive plant's growth and reproduction (Xiao et al. 2019). The ability of *P. americana* to manage water stress by increasing leaf mass per unit area is an indication of its plasticity (Pepe et al. 2022). Plants often suffer adverse effects due to low light levels, but *P. americana* has a competitive advantage over other plants in low light environments in forest understory areas where light resources are limited (Liu et al. 2022). Based on the projected expansion areas of *P. americana*, adaptation to specific environmental condition should be studied to develop effective strategies to combat invasion (Little et al. 2020).

The control of invasive plants focuses on prevention (McMahon et al. 2021). In the areas that were predicted to get increased invasion, such as the Yangtze River Delta region and Fujian, prevention should be the top priority, especially the sensitive sites with high risk of invasion (Tiwari et al. 2022). Human activities have been shown to contribute to the spread of exotic species (Wu et al. 2010). This plant is frequently found in areas frequently visited by people (Fu 2012; Zima and Štefanić 2021), including villages, front lawns, tea gardens, and orchards. Thus, the government should strengthen quarantine and control measures to prevent the spread of invasive species by regulating the movement of goods and people (De Groot et al. 2020). Additionally, the government should create an invasive species information database to improve information exchange and sharing between regions, allowing for timely invasion prediction, risk assessment, and emergency prevention and control measures to prevent the predicted proliferation from becoming a reality.

In this study, the invasion is predicted to be more intense in Sichuan, Guizhou, northeastern Guangxi, southwest Hunan, coastal Fujian on the southeastern coast, northern Taiwan, and southeastern Zhejiang, where it is most likely to occur under current conditions. Accordingly, for chemical control, low concentrations of glyphosate can be sprayed before the fruit setting to effectively control the growth and fruit set of *P. americana* (Cheng et al. 2015). It is recommended that chemical shall be prioritized in Guizhou, Guangxi, and Hunan, where the invasion is most severe. Biological control can be achieved by biological substitution, for instance by using economically or ecologically valuable plants such as *Dolichos lablab* and *Amorpha fruticosa* to enhance interspecific competition and control the spread of invasive plants (Cheng et al. 2015; Wang et al. 2021) Plant allocation structure optimization is also an effective tool to prevent the monopolization of habitats by exotic plants (Luo et al. 2022). According to our simulations of changes in the spatial structure of *P. americana*, eastern Sichuan, Guizhou, northern Guangxi, northern Guangdong, Fujian, Jiangxi, Hubei, southern Hunan, and northern Taiwan are predominantly reserved areas. In these areas, physical, chemical, and biological control methods can be used to curb the rapid spread of *P. americana*. However, physical, chemical, and biological control of invasive alien plants does not prevent re-emergence, which is a problematic aspect of invasive species prevention and control. Therefore, it is also possible to make rational use of the ecological control technology system specific to *P. americana*, such as the plant–microbe feedback mechanism, the chemosensory effect of native plants, and the regulation of ecological factors such as light and water (Liao et al. 2021). Invasive plants can be resourced for scientific means, for example, by utilizing the ability of *P. americana* to absorb metals and transfer them to leaf tissue and by selecting commercial plant species that are adapted to appropriate climate and soil conditions (Máximo et al. 2020; Kim et al. 2008).

The traits of invasive species generally have phenotypic plasticity, but this is not always the case (Davidson et al. 2011). Research on the genomic resources of *P. americana* can be enhanced to use genetic precision to prevent and control invasive (Peng et al. 2019). Research is needed to understand which species of birds feed on the seeds of *P. americana* and what related control measures can stop its spread by the birds (Li et al. 2017). Overall, it is important to identify the factors that influence the plasticity of invasive plants in areas where many loss zones are expected and to exploit these factors to control plant invasions. A well-established risk assessment system, which can be used to effectively control the introduction and spread of invasive alien plants, depends primarily on the availability of information about invasive alien plants and the experience of the assessor. Many of the factors in the system are constantly changing, and as this situation is dynamic (Feng and Zhu 2010), more timely invasion studies will improve the whole system and address inadequate information recording, misidentification, and poor analysis of the habitat of exotic plants in China (Yan et al. 2012) (Additional file 1).

Conclusions

The MaxEnt optimization model was used in this study to predict the potential geographic distribution of *P. americana* under a variety of time periods and climatic conditions. Precipitation and temperature together influenced the distribution pattern of potential risk zones for *P. americana*, with bio6, bio2, bio17, and bio12 being the main factors affecting the distribution of potential risk zones for *P. americana*. All potential risk zones for *P. americana* under the six shared socioeconomic pathways showed upward trends, and an overall trend toward the southeast emerged. The most obvious trend was the expansion of *P. americana* due to continuous warming caused by high-concentration emissions. The study highlights the strong invasive nature of this species in future. Its unique ability to purify the environment and serve as a medicinal plant can be exploited in a rational manner to realize the resource utilization of invasive plants and contribute to the control of invasive plants. According to the predicted results, targeted strategies for the prevention and control of areas with different changes in *P. americana* were developed based on the predicted results.

Abbreviations

CMIP: Coupled Model Intercomparison Project Phase; SSP: Shared Socioeconomic Pathway; AUC: Area under curve; IPCC: Intergovernmental Panel on Climate Change; GHG: Greenhouse gas; ENMs: Ecological Niche Models; BCC-CSM2MR: Beijing Climate Center-Climate System Model-Medium Resolution; CSV: Comma-separated values; SPSS: Statistical Product Service Solutions; RM: Regularization multiplier; FC: Feature combination; AIC: Akaike information criterion; AUC.DIFF: The difference between the training AUC and test AUC values; ASCII: American Standard Code for Information Interchange; PC: Percent contribution; PI: Permutation importance; TRGO: The regularization training gain using the factor alone; TRGW: The regularization training gain using other factors; TGO: The test gain using the factor alone; TGw: The test gain using other factors; AUCw: The area under the receiver operating characteristic curve using other factors; AUC: The area under the working characteristic curve of the subjects using the variable alone; L: Linear; Q: Quadratic; H: Hinge; P: Product; T: Threshold.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-022-00414-9.

Additional file 1: Table S1. 405 species presence data for MaxEnt modeling. **Table S2.** Evaluation metrics of Maxent model generated by ENMeval. **Fig. S1.** avg.diff.AUC. **Fig. S2.** avg.test.AUC. **Fig. S3.** avg.test.or10pct. **Fig. S4.** avg.test.orMTP. **Fig. S5.** delta.AICc. **Fig. S6.** Analysis of omission commission. **Fig. S7.** The receiver operating characteristic (ROC). **Fig. S8.** Jackknife test for the importance of environmental variables.

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Author contributions

YX: visualization, software, methodology, investigation, writing—original draft, formal analysis, project conceptualization, analysis, first draft and editing, data curation, writing—review and editing. XY: visualization, software, methodology, writing—original draft, investigation, formal analysis, data curation, project conceptualization, designing feld layout, writing—review and editing. QY: visualization, investigation, formal analysis, data curation, project conceptualization, literature review, field survey. HW: investigation, conceptualization, field survey. YL: software, project conceptualization, visualization conceptualization, data curation. GZ: investigation, funding acquisition, project conceptualization, field survey. QH: data curation, investigation. TZ: project administration, formal analysis, data curation, developing model through MaxEnt. BL: methodology, investigation, funding acquisition, formal analysis, project conceptualization, writing—review and editing. All authors have read and agreed to the published version of the manuscript. All authors read and approved the final manuscript.

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Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Forestry College, Fujian Agriculture and Forestry University, Fuzhou 350002, Fujian, China. [2]College of Landscape Architecture and Art, Fujian Agriculture and Forestry University, Fuzhou 350002, Fujian, China. [3]Forestry Science and Technology Center of Shunchang County, Shunchang, Nanping 353200, Fujian Province, China.

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