HORTSCIENCE 59(2):179-187. 2024. https://doi.org/10.21273/HORTSCI17390-23

Current and Future Distribution of Camellia sinensis in China Estimated by MaxEnt

Junjun Chen

Suzhou Polytechnic Institute of Agriculture, Suzhou 215008, China

Yawen Yin

College of Forestry, Nanjing Forestry University, Nanjing 210037, China

Wensheng Yu

Jiangsu Taihu Lake Evergreen Fruit Technology Promotion Center, Suzhou Institute of Pomology Science, Suzhou 215000, China

Wenkai Tao, Yajian Huang, and Bailing Zhu

College of Forestry, Nanjing Forestry University, Nanjing 210037, China

Keywords. Camellia sinensis, climate change, latent geographical distribution, MaxEnt model, tea plant, variable selection

Abstract. Tea (Camellia sinensis L.) is an important cash crop. In the context of climate change, analyzing the current distribution of tea trees and climate change environmental variables to predict the potential distribution area of tea trees in the future can help decision-makers make appropriate planting decisions and promote sustainable management. In this study, an optimized MaxEnt model was used to predict the limiting factors of tea tree growth and distribution under current and future climate change scenarios. The climate soil mixing model [area under the curve (AUC) = 0.934] performed excellently. The results showed that precipitation, temperature, slope, and soil factors all affected the distribution of suitable habitats for tea trees. Compared with the current distribution area of tea trees, under three shared socioeconomic pathways (SSP126, SSP245, and SSP585), the area of highly suitable habitats for tea trees will expand, especially in 2061-2080 and 2081-2100 years, and the suitable area will extend overall to the north of China, indicating that future climate change may create more new suitable habitats for tea production, especially in Shandong, Shaanxi, Guizhou, and Yunnan provinces. This study will provide important scientific insights for tea production decision-making, tea garden location selection, and future adaptation methods, and will help in the cultivation and transplantation of tea trees in the future.

Global climate change affects many ecosystems and biota. It not only affects the growth and distribution of vegetation worldwide but also leads to the loss of species diversity and germplasm resources. Climate and habitat change affect vegetation composition and species distribution (Austin and Van Niel 2011), because many common plants, especially herbaceous plants and shrubs, are highly sensitive to climate change (Kane et al. 2017). The prediction of the underlying geographical distribution of species can not only provide the study of flora formation and

Received for publication 11 Sep 2023. Accepted for publication 3 Nov 2023.

Published online 16 Jan 2024.

J.C. and Y.Y. contributed equally to this work and should be considered co-first authors.

This research was funded by the Jiangsu modern agricultural industrial technology system construction project. Grant No. JATS[2022]396.

Y.Y. is the corresponding author. E-mail: <code>yawen_yin@</code> <code>njfu.edu.cn.</code>

This is an open access article distributed under the CC BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/).

origin of species but also can play an important role in genetic improvement. The consequences of climate change include periods of drought, extreme high-temperature weather, and heavy rainfall causing surface soil erosion. This means that the tea planting area and yield are seriously affected by the climate and soil environment, which will make some of the existing tea garden areas unsuitable for tea planting (Su et al. 2017); many studies have described the relationship between climate and plant productivity and species richness.

Camellia is the most abundant and economically valuable genus in the camellia family, among which *Camellia sinensis* L. (Fig. 1A) is one of the representative species. The tea tree has a wide planting area and there is a long history of tea culture in China. Tea, as one of the world's three major nonalcoholic beverages, is deeply loved by people all over the world. In China, tea, as a beverage plant, is an important economic crop and plays an important role in rural poverty reduction and economic growth (Wanyama et al. 2011). Tea is beneficial to human health, containing caffeine, tea polyphenols,

cacopromine, volatile oil, and other ingredients. Tea is used as a daily beverage, which helps digestion, refreshes, strengthens, promotes diuresis, reduces diarrhea and has other functions. Tetranine, an a.i. in tea, reduces the risk of cancer, cancer recurrence, and cardiovascular and neurological diseases. It has beneficial effects in treating chronic diseases (e.g., hypertension, diabetes).

At present, domestic and foreign research into all aspects of tea production and use is increasing year by year, but its distribution and limiting factors are reported less. The growth of tea plants is restricted by climate conditions. In summer, even growing in a shady environment in Suzhou, Jiangsu Province, tea plants can easily wilt or even die because of long-term drought conditions (Fig. 1B and C). This study aims to investigate the plant species in the world and the overall spatial distribution within China, to provide important basic data for the development of tea tree planting, planning, and organization. Considering the rich tea germplasm resources in China, collecting these data is of great significance.

In terms of geographical distribution, tea trees are mainly distributed in the south and southwest, including the provinces, cities, and districts south of the Qinling Mountains and the Huaihe River. The Chinese Academy of Agricultural Sciences divides China into four tea areas according to their ecological and geographical conditions: South China, Southwest China, Jiangnan, and Jiangbei. Wild tea trees are common in mountains or hillside forests below 1000 m. They like deep acidic soil and can also grow well in a rocky soil environment. In China, tea trees are cultivated in mountains, the foothills of mountains, and hilly areas (De Costa et al. 2007). In addition to their economic value, tea trees also have good ecological value; for example, planting tea on barren hills can help to prevent soil erosion (El Kateb et al. 2013).

Climate models can determine the geographic distribution of biological ecosystems, with species ranges often defined by their bioclimatic range (Kopp and Cleland 2014). Currently, there are many ecological models used to describe the potential distribution areas of organisms (Li et al. 2013). In this study, the maximum entropy method (maximum entropy model, MaxEnt) was used to predict the potential distribution of Camellia sinensis. As the species distribution model (SDM) based on the maximum entropy theory, MaxEnt selects the distribution with the largest entropy from the appropriate distribution center as the optimal distribution. Since its development in 2006, it has been widely used in the prediction of endangered species, species distribution under future climate change, and the identification of invasive species monitoring areas (Lissovsky and

Changes in the species range are a generally expected consequence of global warming (Renwick and Rocca 2015). Combining species occurrence data and literature and tea tree growth environment data, we can predict

the potential geographical distribution of the species in the future, with high precision and stability even based on small samples (Elith et al. 2011). On this basis, this study combines the MaxEnt model, ENMTools, R language, and geographic information system (ArcGIS) to predict the suitable habitat and its centroid trajectory under current and future climate change scenarios, to further understand the distribution characteristics of the species and its ecological adaptability, and provide a scientific basis for the protection of tea tree resources and the introduction of tea trees into new regions.

Materials and Methods

Species location data. Through China Digital Herbarium (http://www.cvh.ac.cn/), Teaching Specimen Sharing Platform (http://mnh.scu. edu. cn/), Global Biodiversity Information Service Network (https://www.gbif.org/), and other digital platforms, we extracted tea tree specimen data and screened and eliminated specimens with missing coordinates or repeated data (Huang et al. 2020). To reduce the error of clustering effects in predicting the underlying distribution region and reduce model overfitting, we selected only one sample record in the grid range of 2.5 "2.5" (Yan et al. 2021). Finally, 1243 points were selected for further analysis (Fig. 2).

Environment variables. With the coupled model intercomparison project phase 6 (CMIP 6) planned (Wu et al. 2021), the output results of the new generation of the atmospheric circulation model [general circulation model (GCM)] have been released successively. The sharing economy path, Shared Socioeconomic Pathway (SSP) replaces the original RCP mode, showing the new emission scenario driven by different social and economic models. It is crucial to explore chronologically the change patterns of future precipitation and temperature in China under the new model. The climate data of v2.1 were downloaded from the World Meteorological Database (http://www.worldclim.org/) from 1970 to 2000, with 19 bioclimatic factors of environmental variables correlated with temperature (Bio01~Bio11) and precipitation (Bio12~ Bio19), and elevation data were selected with a spatial resolution of 2.5 arc-minutes.

Future climate data were obtained from the global climate model of CMIP 6 (BCC-CSM 2-MR, Beijing climate center climate system model), which Chinese researchers often use to assess species distribution. In previous studies, researchers simulated different shared socioeconomic pathways that explain different degrees of future climate change (Hamed et al. 2022). With the increase in emission intensity, the warming trend is more and more significant; that is, the warming trend is ranked from strong to weak in SSP585, SSP370, SSP245, and SSP126 (Hamadamin and Khwarahm 2023). Three periods are selected to predict the potential distribution of tea trees in the future: 2050s (average 2041–2060), 2070s (average 2061-2080), and 2090s (average 2081-2100). Moreover, assuming the soil and terrain factors will remain constant over the next few decades, this study used the climate factors



Fig. 1. Appearance and leaves (A) of *Camellia sinensis*. (B) Wilting leaves in summer. (C) Pictures of tea plants suffering from natural disasters.

for the future period, and the climate, soil, and terrain factors from the current period. Digital Elevation Model (DEM) elevation data were downloaded from the Geospatial Data Cloud website (http://www.gscloud.cn/), and slope data

were extracted with ArcGIS10.8 software. Seventeen topsoil factors (0~30 cm) were derived from the World Soil Database [Harmonized World Soil Database (HWSD)] (http://www.fao.org/soils-portal/en/).

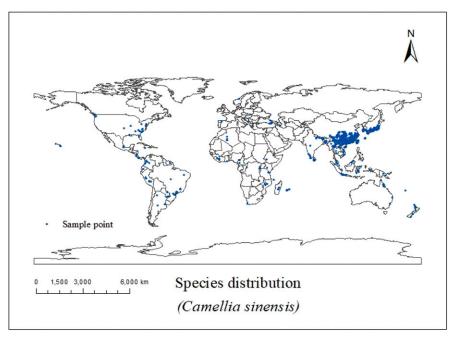


Fig. 2. Distribution points of Camellia sinensis L.

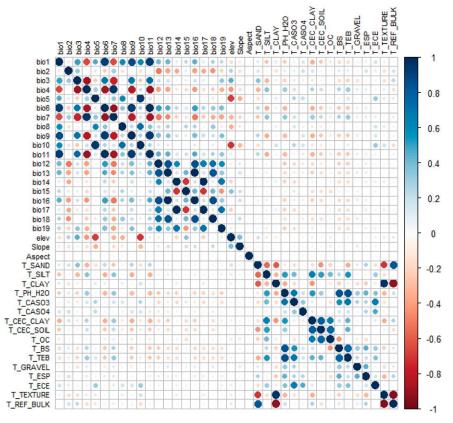


Fig. 3. Pearson correlations of the variables. The blue circles represent positive correlations and the red ones negative. The stronger the correlation, the larger the size of the circle and the darker the color.

Model development and the current habitat prediction. The multicollinearity of the variables may affect prediction accuracy (Li et al. 2023). To avoid the correlation between various climate variables causing overfitting and affecting the accuracy of prediction, Pearson correlation analysis was conducted using ENM-Tools1.4.3 for the collated data, and R3.6.3 software (Fig. 3). For highly correlated variables (correlation coefficient >0.8), only one variable more suitable for model interpretation was selected for the subsequent model prediction (Bian and Shi 2019) (Table 1).

The kuenm software package in R v3.6.3 was used in this study (Cobos et al. 2019) to optimize the implementation of the MaxEnt model. The predictive performance of the model is affected by two parameters that

need to be optimized: the regularization multiplier (RM) and the feature combination (FC). Using these two parameters, the value of RM was set to 0.1 to 4.0, adding 0.1 each time, for a total of 40 regulatory frequencies. The MaxEnt model provides a combination of five element types; namely, linear (linear features, L), quadratic (quadratic features, Q), product (product features, P), fragmentation (hinge features, H), and threshold (threshold features, T) and FC, a total of 29 types. Finally, the preceding 1160 candidate models were tested with the kuenm software package.

The best model was selected according to the following criteria: 1) the significance model, and 2) the omission rate was below 5%. Then, the model with the smallest AICc value (i.e., delta AICc = 0) is the final model. After the

Table 1. Fifteen environment variables used for the MaxEnt model.

Data type	Parameter	Full name or description
Climate factor	Bio2	Mean diurnal range [mean of monthly (max temp - min temp)] (°C)
	Bio3	Isothermality (BIO2/BIO7) (× 100) (%)
	Bio6	Min temperature of coldest mo. (°C)
	Bio11	Mean temperature of coldest quarter (°C)
	Bio12	Annual precipitation (mm)
	Bio14	Precipitation of driest mo. (mm)
	Bio15	Precipitation seasonality (CV)
	Bio16	Precipitation of wettest quarter (mm)
	Bio18	Precipitation of warmest quarter (mm)
Terrain	slope	Slope (°)
Soil factor	T_ESP	Exchangeable sodium percentage in the topsoil (%)
	T_GRAVEL	Volume percentage of gravel in the topsoil (% wt.)
	$T_PH_H_2O$	Soil reaction of topsoil $[-log(H+)]$
	T_SAND	Percentage of sand in the topsoil (%)
	T_CASO4	Top layer sulfate content (% wt.)

model operation, the main ecological factors affecting the distribution of tea trees were evaluated according to their respective contribution rates and the results of a Jackknife test. In practice, AUC indicators derived from the ROC (subject-operating characteristic) are usually used to evaluate the performance indicators of the model (Xu et al. 2020). The AUC value of the curve ROC is a composite indicator of the sensitivity and specificity of the model (Gebrewahid et al. 2020). AUC values range from 0 to 1, with larger values indicating higher confidence in the results.

For the outcome of the predicted completion, the grid values were graded by the maximum test sensitivity (MTSPS) method to categorize the suitability level for the distribution of tea trees in the study area. The data generated by the MaxEnt software were imported into ArcGIS v.10.8. We obtained the potential distribution of suitable habitats for tea trees (P > 0.2326). According to the manual classification method, the distribution area of the tea tree was classified as follows: unsuitable areas ($0.4 < P \le 0.2326$); Slightly suitable areas ($0.4 < P \le 0.56$); and Highly suitable areas ($0.56 < P \le 1$).

Changes in suitable habitat area and centroids. Assessing the suitability of land for tea cultivation is a crucial step in identifying the environmental constraints for sustainable tea production. We predicted the spatial distribution of suitable habitats in China during the current period (1971–2000) and three future periods (2050, 2070, and 2090), using three climate change scenarios (SSP126, SSP 245, and SSP 585). We then compared the changes in area and spatial extent of these predicted suitable habitats across different periods.

To further investigate the trends, we used a Python-based GIS toolkit and SDM toolbox to calculate the centroids of current and future climate distribution areas (Brown 2014; Jin et al. 2022), as well as the total suitable area and high-suitable area. We also calculated the centroid migration distances.

Results

Optimal model and accuracy evaluation. The potential distribution area of the tea plant in China was simulated, using the MaxEnt model. When the model is set to the default parameters, delta AICc is 354.747, but when set to the optimization parameters (FC = QT, RM = 4), delta AICc is 0 (Table 2), AUC.diff is 0.0019. The difference decreases by 67.86%, and the omission rate decreases by 75%, indicating that the degree of overfitting at the optimized parameter setting is lower than the default parameters. The optimized parameters (FC = QT, RM = 4) were used to reconstruct the model and simulate the suitable area for tea trees in China, with the average training AUC at 0.979. The software simulation results show that the MaxEnt model effectively predicts the geographical distribution of tea trees in China.

Current potential distribution area. The distribution area of tea trees in China is 122

Table 2. Evaluation metrics of the default and optimal MaxEnt models by kuenm package.

Setting	FC	RM	AUC.diff	Omission rate	Delta AICc	AICc
Default	LQPH	1	0.0025	0.1271	354.7474	5104.2810
Optimized	QT	4	0.0019	0.0909	0.0000	4760.2058

11'-91 43' E, 35 54'-18 11' N, mainly concentrated in southeast China. Its distribution range includes the southeast of Sichuan Province, Chongqing, Yunnan, Guizhou, Hunan, Hubei, Henan, Anhui, Guangxi, Guangdong, Fujian, Jiangxi, Shandong, Shanxi Province, Jiangsu, Anhui, Zhejiang, Hainan, Taiwan,

and Hong Kong, with almost all sample points distributed in the suitable habitat area for the tea tree (Fig. 2). This suggests that the model can simulate the potential distribution of tea trees.

According to the calculation results of the prediction model and the actual distribution

of sampling points, it can be seen that due to the limitation of climatic conditions, northwest and northeast China are not suitable for the growth of tea trees (75.7% of the national area, a total area of 7,266,300 km²). These unsuitable regions include Tibet, Xinjiang, Qinghai, Gansu, Inner Mongolia, Ningxia, northwestern Sichuan, northern Shaanxi, Shanxi, Hebei, northern Henan, northwestern Shandong, Liaoning, Jilin, Heilongjiang, and other regions. The slightly suitable habitat of tea trees accounts for 2.9% of the total national area (i.e., 279,100 km²). This region is located at the junction of the subtropical

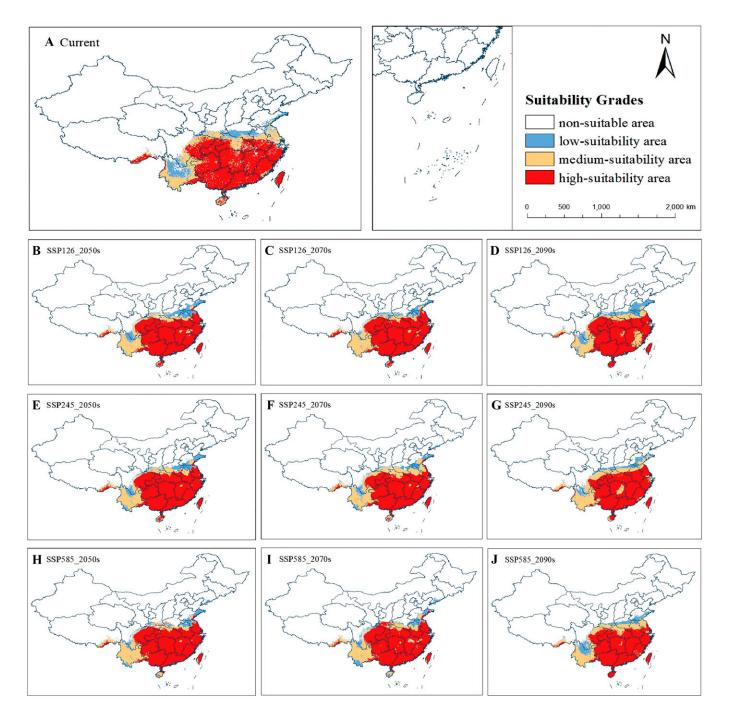


Fig. 4. The current and future potential geographical distribution of *Camellia sinensis* by the 2050s, 2070s, and 2090s according to the climate scenarios SSP 126, SSP245, and SSP 585 based on optimized parameters. (A) Current; (B) SSP126–2050s; (C) SSP126–2070s; (D) SSP126–2090s; (E) SSP245–2050s; (F) SSP245–2070s; (G) SSP245–2090s; (H) SSP 585–2050s; (I) SSP 585–2070s; (J) SSP 585–2090s.

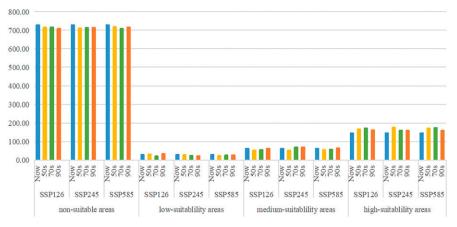


Fig. 5. Changes of suitable habitat area of Camellia sinensis L. under three different climate scenarios (SSP265, SSP245, and SSP585) in current times, the 2050s, 2070s, and 2090s.

monsoon and temperate monsoon climate with the plateau alpine climate. The medium-suitability habitat accounts for 6.3% of the total area of China, a total area of 608,700 km², and highly suitable habitats account for 15.1% of the total land area, of 1,445,900 km².

Future changes in the suitable habitat area. Compared with the current distribution of suitable habitats, the total area of suitable habitats will increase in the future. As shown in Figs. 4 and 5, under three different emission scenarios (SSP126, SSP245, and SSP585), the area of suitable habitats will increase by 1.42%, 1.84%, and 1.15%, respectively, in the 2050s; by 1.23%, 1.64%, and 1.15%, respectively, in the 2070s; and by 2.09%, 1.53%, and 1.24%, respectively, in the 2090s. The high-suitability habitat areas also show a trend of future expansion. It is expected that by the 2050s, under three scenarios, the area of high-suitable habitats will increase by 2.17%, 3.08%, and 2.56%, respectively; compared with the current area, by the 2070s, it will increase by 2.66%, 1.45%, and 2.93%, respectively; and by the 2090s, it will increase by 1.65%, 1.43%, and 1.32%, respectively. Overall, the area of low-suitable habitats fluctuates with climate patterns, the intermediate-suitable habitats begin to differentiate, and the high-suitable areas increase.

Analysis of the change in the spatial pattern. To explain the distribution of future displacement and the direction of changes, we used the centroid analysis, Centroid Changes in the SDM Toolbox v2.5 package to track the centroid trajectory changes of tea tree suitability, with distribution regions over time in different greenhouse gas emission scenarios. Regardless of the greenhouse gas emission scenario, from the current to the future (2090s), the centroid of the total suitable habitat area of tea trees migrates northwest from Huaihua city, Hunan province (27 25'18.03"N, 110 32'34.45"E), and the total area of suitable habitat expands northward, while the total area in the south gradually decreases (Fig. 6). In the SSP126, SSP245, and SSP585 modes, in the 2050s, it moves northwest by 20.09 km, 32.31 km, and 30.36 km, respectively. From the present to

the 2070s, the center of mass continues to move northwest at 33.00 km, 41.19 km, and 50.86 km. By the 2090s, the whole direction shifts to the northeast, by a distance of 23.61 km, 32.08 km, and 30.78 km, respectively. In general, the trajectory distance and direction of the centroids vary over time under different greenhouse gas emission scenarios, and the high-suitability region will expand to the northeast, as shown in Fig. 7. At present, the centroid of the high-suitability area is located in Shaoyang County, Shaoyang City, Hunan Province (111 34'2.438" N, 26 59'30.106" E). In all three climate models, the migration of the high fitness zone was to the northeast, and in the SSP126 model, 2050s, 2070s, and 2090s movement was 69.07 km, 80.79 km, and 54.74 km, respectively. In SSP245 mode, the migration distances until the 2050s, 2070s, and 2090s were 84.73 km, 69.31 km, and 103.11 km, respectively. Under SSP585, the 2050s, 2070s, and 2090s migration distances were 91.89 km, 100.13 km, and 62.05 km, respectively. These results suggest that the movement of centroids is consistent with the spatial pattern changes of suitable areas predicted by the MaxEnt model (Fig. 8) (Zhang et al. 2023).

Discussion

The MaxEnt model has been widely used in ecology, biology, evolutionary biology, and invasive species management (Phillips et al. 2006). It has the advantages of a wide application range, high accuracy, simple operation, low sample number requirements, and stable operation results (Jiangying et al. 2022). Tea is the most popular beverage plant, with a vital economic value (Xue et al. 2013). As a plant native to China and introduced globally, the key environmental factors influence or restrict its growth. According to the results of the knife-cutting method and the contribution rates of climate and soil variables calculated by the model, the main environmental factors affecting the change in tea distribution were determined.

Predicted habitat suitability considering both climatic and soil variables. The prediction results suggest that the variables affecting the suitable area for tea cultivation are as follows: the precipitation during the hottest season (bio18), the average temperature during the coldest season (bio11), and the annual precipitation (bio12). The contribution rates of these three biological climate variables are 50.9%, 20.2%, and 12.0% respectively, with a cumulative value of 83.1% (Table 3). Generally, when the probability of tea tree existence exceeds 0.5 (Gebrewahid et al. 2020), the corresponding ecological factors are suitable for plant growth (Jia et al. 2019). Precipitation is an important factor for the survival and growth of tea seedlings and is also one of the essential factors for most plants. Abundant rainfall significantly increases the soil water content near the planting location, providing a good growing environment for water-demanding tea trees. In arid environments, the transpiration rate of tea tree leaves is high, and even a short period of drought can cause leaf edges to dry and necrosis to occur, leading to a decrease in yield, quality, and economic value (Waheed et al. 2012). In addition, temperature is crucial for normal plant growth. When tea trees are subjected to prolonged heat stress, a series of changes occur in their internal physiological mechanisms (Bita and Gerats 2013). If heat stress is brief, plants can regulate osmotic adjustment substances to protect enzyme activity; however, when the stress duration increases beyond a certain point, the damage is irreversible. Conversely, when the environmental temperature decreases, it remains below the minimum temperature for plant growth, resulting in freezing damage. These factors not only limit the geographical distribution of plants but also seriously affect the yield and economic value of tea. When the precipitation during the hottest season reaches 2600 mm (bio18), the probability of tea tree existence tends to plateau. The appropriate precipitation range for the hottest season (bio18) is 500 to 2900 mm. The suitable range for annual precipitation (bio12) is 1300 to 2300 mm. The probability of tea tree existence increases with an increase in the minimum temperature during the coldest month (bio11). The predicted suitable growing condition for tea trees is 2 to 10 °C.

The main soil factors affecting the growth of tea trees are the percentage of exchangeable sodium in the topsoil (T_ESP) and the percentage of gravel by volume in the topsoil (T_gravel). Exchangeable Sodium Saturation Percentage (ESP), also known as alkalinization, is an important indicator to determine whether the soil is alkaline. Generally speaking, the higher the ESP, the higher the degree of soil alkalinization, and the worse the soil traits (Cemek et al. 2007). Predictive analysis shows that if the ESP value is greater than 2%, the tea tree survival rate will be less than 50%. This is consistent with the tea tree's preference for less acidic soils (Ye et al. 2023). T_gravel is closely related to soil permeability; soil with high sand content has

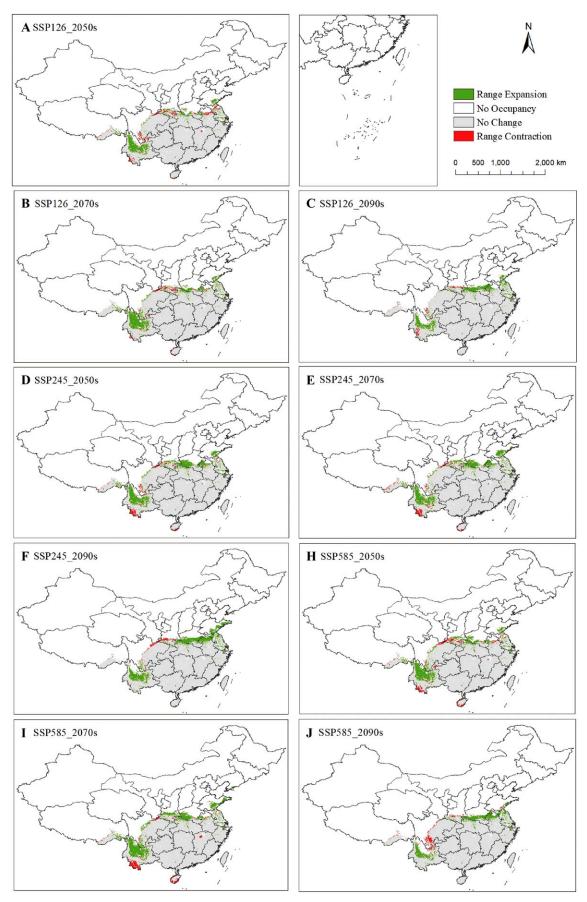


Fig. 6. Comparison of changes in the spatial pattern of total suitable *Camellia sinensis* habitat under three different climate scenarios (SSP126, SSP245, SSP585) in the 2050s, 2070s, and 2090s. Total suitable area change: green represents expansion areas, red represents contraction areas, gray represents unchanged areas, and white represents unsuitable areas.

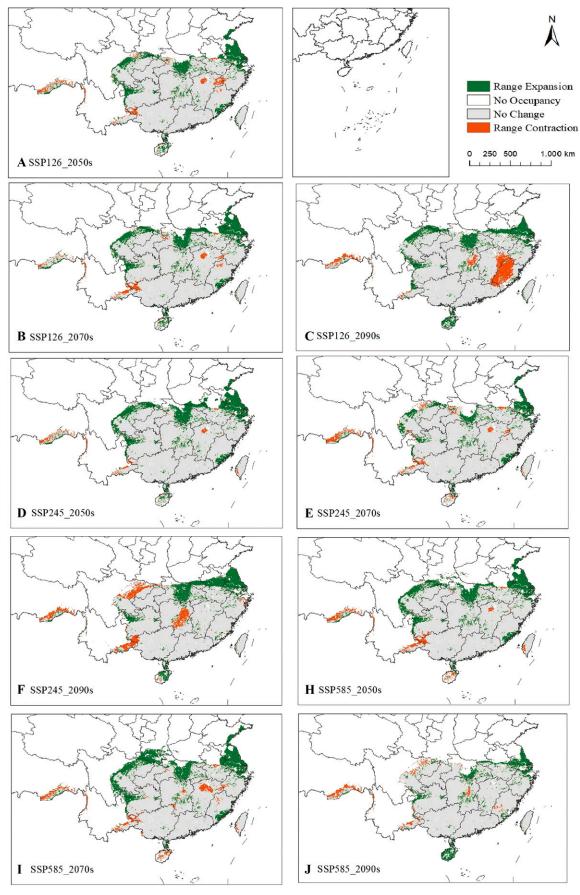


Fig. 7. Spatial pattern of the *Camellia sinensis* high-suitability habitat area in the 2050s, 2070s, and 2090s under three different climate scenarios (SSP126, SSP245, SSP585). High-suitability area change: green represents expansion areas, red represents contraction areas, gray represents unchanged areas, and white represents unsuitable areas.

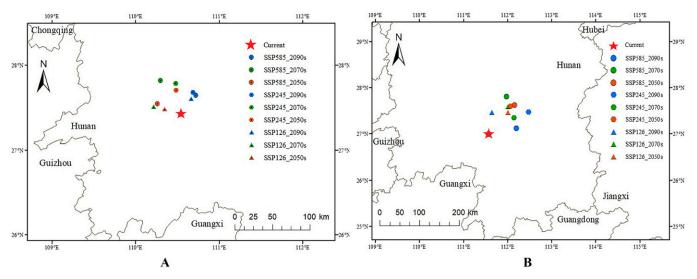


Fig. 8. Distance moved by the centroid of *Camellia sinensis* under three different climate scenarios (SSP126, SSP245, SSP585) in the future. [The centroid of total suitable habitat (**A**) and the centroid of high-suitability habitat (**B**) are distinguished by the center of symbols.] Climate scenarios are distinguished by a given symbol; for time periods, the current time is displayed by a red star, and the 2050s, 2070s, and 2090s are distinguished by a given color.

high porosity and increased root permeability (Chen et al. 2020).

In addition, slope is also an important factor affecting the growth of tea trees. The slope is closely related to light and soil properties. Compared with flat land, on a slope, the angle of the light changes, the time of daylight is reduced, and the organic carbon content and soil depth are low (Khormali et al. 2007) (Supplemental Appendix 1).

The tea tree is a kind of cash crop dependent on picking tender buds. Continuous low temperature or high temperature, salt and alkali, soil hardening, and sun exposure will seriously damage the growth of the tea tree, affecting the appearance and drinking quality of tea, thus greatly reducing the attractiveness of tea to consumers. All of these influencing factors correspond to the main limiting factors screened here. Therefore, in the border area of the subtropical monsoon climate, temperate monsoon climate, and plateau and alpine climate, the climate conditions change greatly, and the distribution pattern of tea trees will continue to change in the future. The existing research results can provide a reliable theoretical basis for the prediction of the MaxEnt model. However, the predictions of this model are faster and more systematic than conventional experimental methods (Ashraf et al. 2016).

Changes in the spatial pattern and centroid distribution of potential tea trees. The predicted overall change in the suitable habitat area for tea trees is as follows. From now to he 2090s, the total area of suitable habitat continues to expand with the increase of greenhouse gas emissions. In the high-concentration emission scenario, SSP585, the tea habitat in the high-suitability area will increase with increasing CO₂ concentration in the second half of the 21st century. Under the climate change scenario, the center of mass can reflect the distance and direction and play a key role in determining the spatial distribution of land, so in different periods, the suitable habitat for tea trees will be considered as a whole. The results of centroid analysis show that the centroid of the total suitable habitat for tea trees is currently located in Xupu County, Huaihua City, Hunan Province (110 32'34.454" N, 27 25'18.026" E). The centroid of the highsuitability habitat is located in Shaoyang County, Shaoyang City, Hunan Province (111 34'2.438" N, 2659'30.106" E). The predicted center of the total suitable area for tea trees shows that in three different greenhouse gas emission scenarios, it meets the trend of northward migration (2050s, 2070s, 2090s), which is in line with previous research conclusions. Combining the trajectory, distance, and direction of the centroids in different periods, we speculate that the

centroid does not always move in the same direction, and the smaller the period, the more complex the trajectory, as has been found in previous plant studies. The environmental requirements of plant distribution in the central region of tea trees may differ from the plants in marginal areas.

To better understand the distribution of tea plants in the future, we need to further study the ecological and physiological mechanisms of their adaptation to environmental factors. Compared with the current climate scenario, the potential distribution pattern of tea trees in China is not obvious, and there is no extensive migration, but the distribution of tea trees in Yunnan, Sichuan, Hebei, Shandong, and other provinces is decreasing. Therefore, it is necessary to take timely measures, such as establishing local protection areas and constructing ex situ conservation sites to effectively protect the plant resources of tea trees, which is of great significance to the collection of new species of this genus, germplasm preservation, and protection of the diversity of this genus.

Study limitations. Most SDMs infer species' environmental conditions based on observed species occurrence data. However, we cannot simply equate the habitat of species occurrence data with the suitable habitat of the species. That is to say, the fact that a region has a suitable habitat predicted by the model does not necessarily mean that the species is found there (Elith and Leathwick 2009). In addition, biological factors such as human activities and species interactions also need to be considered during environmental factor selection (García-Valdés et al. 2015). In future research, to better predict the distribution of tree species, we will study the comparison and convergence of multiple models or design better algorithms to improve the overall analysis of species diversity and trends in unique groups.

Table 3. Contribution of the environmental predictors influencing the probability of distribution of *Camellia sinensis* in China.

Climate variables	Percentage contribution (%)	Soil variables	Percentage contribution (%)
bio18	50.9	t_gravel	2.4
bio12	20.2	t_esp	1.6
bio11	12.0	slope	1.4
Bio16	3.6	t_sand	0.5
Bio6	3.4	t_CaSO ₄	0.2
bio14	1.8	t_ ph_H ₂ O	0.1
Bio2	0.9		
bio15	0.8		
Bio3	0.3		

Conclusion

To address the challenges of climate change to China's tea industry, an ecological niche model for tea trees was constructed, and the suitable habitat for tea trees was predicted in combination with climate and soil factors. The SDM performed well with a high degree of credibility in model prediction. Based on the prediction of the MaxEnt model, with the enhancement of the global greenhouse effect, most plants growing in the northern hemisphere will migrate to higher latitudes in the future, and their suitable habitat area will gradually expand. In all three assumed emission scenarios, the suitable habitat areas for tea trees will extend northward. Tea plantation enterprises and germplasm resource research units should consider the predicted changes and plan new suitable areas for tea trees. The relevant departments should formulate reasonable and sustainable land use plans according to local conditions, leaving enough space for eventual migration. Based on the environmental factors limiting the distribution of tea trees, artificial environments suitable for their growth can be created, and even artificial afforestation can be carried out to maximize the economic value of tea trees while protecting suitable habitats and providing shelter for tea trees to adapt to climate change.

References Cited

- Ashraf U, Ali H, Chaudry MN, Ashraf I, Batool A, Saqib Z. 2016. Predicting the potential distribution of *Olea ferruginea* in Pakistan incorporating climate change by using Maxent Model. Sustainability. 8(8):1–11. https://doi.org/10.3390/su8080722.
- Austin MP, Van Niel KP. 2011. Improving species distribution models for climate change studies: Variable selection and scale. J Biogeogr. 38(1):1–8. https://doi.org/10.1111/j.1365-2699.2010.02416.x.
- Bian X, Shi F. 2019. Predicting the potential distribution of Rhaphidophorinae (Orthoptera, Rhaphidophoridae) in China. Zootaxa. 4683(1): 120–128. https://doi.org/10.11646/zootaxa.4683.1.6.
- Bita CE, Gerats T. 2013. Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stresstolerant crops. Front Plant Sci. 4:1–18. https://doi.org/10.3389/fpls.2013.00273.
- Brown JL. 2014. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol. 5(7):694–700. https://doi.org/10.1111/2041-210X.12200.
- Cemek B, Güler M, Kiliç K, Demir Y, Arslan H. 2007. Assessment of spatial variability in some soil properties as related to soil salinity and alkalinity in Bafra plain in northern Turkey. Environ Monit Assess. 124(1–3):223–234. https://doi.org/10.1007/s10661-006-9220-y.
- Chen XC, Chen R, Wu YF, Wang Y. 2020. Research on the geological background of tea planting in Duyun City based on RS and GIS. Remote Sens L Resour. 32(1):224–231. https://doi.org/10.6046/gtzyyg.2020.01.30.
- Cobos ME, Townsend Peterson A, Barve N, Osorio-Olvera L. 2019. Kuenm: An R package for detailed development of ecological niche models using Maxent. PeerJ. 7:e6281. https://doi.org/10.7717/peerj.6281.
- De Costa WAJM, Mohotti AJ, Wijeratne MA. 2007. Ecophysiology of tea. Braz J Plant Physiol.

- 19(4):299–332. https://doi.org/10.1590/S1677-04202007000400005.
- Elith J, Leathwick JR. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst. 40:677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of Max-Ent for ecologists. Divers Distrib. 17(1):43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.
- García-Valdés R, Svenning JC, Zavala MA, Purves DW, Araújo MB. 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. J Appl Ecol. 52(4): 902–912. https://doi.org/10.1111/1365-2664. 12453.
- Gebrewahid Y, Abrehe S, Meresa E, Eyasu G, Abay K, Gebreab G, Kidanemariam K, Adissu G, Abreha G, Darcha G. 2020. Current and future predicting potential areas of Oxytenanthera abyssinica (A. Richard) using MaxEnt model under climate change in Northern Ethiopia. Ecol Process. 9(1):6. https://doi.org/10.1186/ s13717-019-0210-8.
- Hamadamin BA, Khwarahm NR. 2023. Mapping impacts of climate change on the distributions of two endemic tree species under socioeconomic pathway scenarios (SSP). Sustainability. 15(6):5469. http://doi.org/10.3390/su15065469.
- Hamed MM, Nashwan MS, Shahid S. 2022. A novel selection method of CMIP6 GCMs for robust climate projection. Int J Climatol. 42(8): 4258–4272. http://doi.org/10.1002/joc.7461.
- Huang HL, Zhong WG, Yi DP, Cai J, Zhang L. 2020. Predicting the impact of future climate change on the distribution patterns of *Toona ciliata* var. *pubescens* in China. J Nanjing For Univ Sci Ed. 44(3):163–170. https://doi.org/10.3969/j.issn.1000-2006.201812037.
- Jia X, Wang C, Jin H, Zhao Y, Liu L, Chen Q, Li B, Xiao Y, Yin H. 2019. Assessing the suitable distribution area of *Pinus koraiensis* based on an optimized MaxEnt model. Shengtaixue Zazhi. 38(8):2570–2576. https://doi.org/10.13292/j.1000-4890.201908.017.
- Jiangying G, Gang H, Yali Y, Li H. 2022. Maxent model predictions of climate change impacts on the suitable distribution of crayfish aquaculture in China. Indian J Anim Res. 56(10): 1295–1300. https://doi.org/10.18805/IJAR.BF-1472.
- Jin Z, Yu W, Zhao H, Xian X, Jing K, Yang N, Lu X, Liu W. 2022. Potential global distribution of invasive alien species, Anthonomus grandis Boheman, under current and future climate using optimal MaxEnt model. Agriculture. 12(11): 1759. https://doi.org/10.3390/agriculture12111759.
- Kane K, Debinski DM, Anderson C, Scasta JD, Engle DM, Miller JR. 2017. Using regional climate projections to guide grassland community restoration in the face of climate change. Front Plant Sci. 8:1–11. https://doi.org/10.3389/fpls.2017.00730.
- El Kateb H, Zhang H, Zhang P, Mosandl R. 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: A field experiment in Southern Shaanxi Province, China. Catena. 105:1–10. https://doi.org/10.1016/j.catena. 2012.12.012.
- Khormali F, Ayoubi S, Foomani FK, Fatemi A. 2007. Tea yield and soil properties as affected by slope position and aspect in Lahijan area, Iran. Int J Plant Prod. 1(1):98–111.
- Kopp CW, Cleland EE. 2014. Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. J Veg Sci. 25(1):135–146. https://doi.org/10.1111/jvs.12072.

- Li D, Li Z, Liu Z, Yang Y, Khoso AG, Wang L, Liu D. 2023. Climate change simulations revealed potentially drastic shifts in insect community structure and crop yields in China's farmland. J Pest Sci. 96(1):55–69. https://doi.org/ 10.1007/s10340-022-01479-3.
- Li GQ, Liu CC, Liu YG, Yang J, Zhang XS, Guo K. 2013. Advances in theoretical issues of species distribution models. Acta Ecol Sin. 33(16):4827–4835.
- Lissovsky AA, Dudov SV. 2021. Species-distribution modeling: Advantages and limitations of its application. 2. MaxEnt. Biol Bull Rev. 11(3):265–275. https://doi.org/10.1134/s2079086421030087.
- Phillips SB, Aneja VP, Kang D, Arya SP. 2006. Modelling and analysis of the atmospheric nitrogen deposition in North Carolina. Int J Glob Environ Issues. 6(2–3):231–252. https://doi.org/10.1016/j.ecolmodel.2005.03.026.
- Renwick KM, Rocca ME. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. Glob Ecol Biogeogr. 24(1):44–51. https://doi.org/10.1111/geb.12240.
- Su S, Wan C, Li J, Jin X, Pi J, Zhang Q, Weng M. 2017. Economic benefit and ecological cost of enlarging tea cultivation in subtropical China: Characterizing the trade-off for policy implications. Land Use Policy. 66(129):183–195. https://doi.org/10.1016/j.landusepol.2017.04.044.
- Waheed A, Hamid FS, Shah AH, Ahmad H, Khalid A, Abbasi FM, Ahmad N, Aslam S, Sarwar S. 2012. Response of different tea (*Camellia sinensis* L.) clones against drought stress. J Mater Environ Sci. 3(2):395–410.
- Wanyama FO, Develtere P, Pollet I. 2011. Encountering the evidence: Cooperatives and poverty reduction in Africa. Working Papers on Social and Co-operative Entrepreneurship WP-SCE 08-02. https://doi.org/10.2139/ssrn.1330387.
- Wu T, Yu R, Lu Y, Jie W, Fang Y, Zhang J, Zhang L, Xin X, Li L, Wang Z, Liu Y, Zhang F, Wu F, Chu M, Li J, Li W, Zhang Y, Shi X, Zhou W, Yao J, Liu X, Zhao H, Yan J, Wei M, Xue W, Huang A, Zhang Y, Zhang Y, Shu Q, Hu A. 2021. BCC-CSM2-HR: A high-resolution version of the Beijing Climate Center Climate System Model. Geosci Model Dev. 14(5):2977–3006. https://doi.org/10.5194/gmd-14-2977-2021.
- Xu N, Meng F, Zhou G, Li Y, Wang B, Lu H. 2020. Assessing the suitable cultivation areas for *Scutellaria baicalensis* in China using the Maxent model and multiple linear regression. Biochem Syst Ecol. 90:104052. https://doi.org/ 10.1016/j.bse.2020.104052.
- Xue H, Ren X, Li S, Wu X, Cheng H, Xu B, Gu B, Yang G, Peng C, Ge Y, Chang J. 2013. Assessment of private economic benefits and positive environmental externalities of tea plantation in China. Environ Monit Assess. 185(10):8501–8516. https://doi.org/10.1007/s10661-013-3191-6.
- Yan X, Wang S, Duan Y, Han J, Huang D, Zhou J. 2021. Current and future distribution of the deciduous shrub *Hydrangea macrophylla* in China estimated by MaxEnt. Ecol Evol. 11(22): 16099–16112. https://doi.org/10.1002/ece3.8288.
- Ye J, Wang Y, Lin S, Wang Y, Chen P, Hong L, Jia X, Kang J, Wu Z, Wang H. 2023. Metabolomics analysis of the effect of acidification on rhizosphere soil microecosystem of tea tree. Front Plant Sci. 14:1–12. https://doi.org/10.3389/fpls.2023.1137465.
- Zhang H, Sun X, Zhang G, Zhang X, Miao Y, Zhang M, Feng Z, Zeng R, Pei J, Huang L. 2023. Potential global distribution of the habitat of endangered *Gentiana rhodantha* Franch: Predictions based on MaxEnt ecological niche modeling. Sustainability. 15(1):631. https://doi.org/10.3390/ su15010631.