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Predicting current and future potential distribution of *Changnienia amoena* in China under global climate change

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Changnienia amoena is a terrestrial orchid endemic to China and holds significant ornamental and medicinal value. Understanding the current and future potential geographic distribution patterns of _C. amoena_ under climate change is crucial for its effective conservation and sustainable development. This study uses 48 distribution records and 19 environmental variables to simulate and predict the potential distribution and spatial pattern changes of _C. amoena_ under different future gas emission scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5) for both the 2050s and 2090s. The dominant environmental variables influencing its distribution were also identified. The MaxEnt model yielded an AUC of 0.990 and CBI of 0.959, indicating extremely high predictive accuracy. The key environmental variables influencing the distribution of _C. amoena_ include the minimum temperature of coldest month (Bio06), annual precipitation (Bio12), isothermality (Bio03), land use classification, slope, topsoil USDA texture classification, elevation, and topsoil calcium carbonate. Among these, temperature and precipitation have relatively significant impacts on the distribution of _C. amoena_. Under the SSP1-2.6 scenario, the suitable habitat for _C. amoena_ shows a slight contraction, while under the SSP2-4.5 and SSP5-8.5 scenarios, the suitable habitat shifts and expands significantly towards the northwest, higher latitude and altitude areas. This research has important scientific significance and practical guidance value for the in-situ conservation, ex-situ cultivation, and sustainable utilization of _C. amoena_.

The rapid escalation of anthropogenic greenhouse gas emissions has pushed global temperatures to unprecedented heights, with the Intergovernmental Panel on Climate Change (IPCC) reporting a 1.1 °C increase in average planetary temperature since pre-industrial times—a critical threshold in humanity's unfolding climate narrative[1]. If effective emission reduction measures are not implemented, the global average temperature is projected to reach or exceed 1.5 °C by 2030. As global warming intensifies, extreme weather events such as extreme high/low temperatures, droughts, and floods are becoming increasingly frequent, inevitably impacting global ecosystems and biodiversity[2]. These impacts include biodiversity loss, shifts in species distributions, disruptions to ecosystem functions, and insufficient natural resource supply.

Orchidaceae, one of the most species-rich yet highly threatened plant families[3–5], exhibits unique characteristics such as reliance on specific symbiotic fungi for nutrients and specialized pollinators for reproduction[6]. These traits, along with their narrow ecological preferences and restricted distribution ranges, make them particularly sensitive to climate change. Narrowly distributed species are generally more vulnerable to the effects of climate change[7]. Different orchid species may respond differently to global warming. For example, among four European species of the genus *Orchis*, three species (*O. anthropophora*, *O. purpurea*, and *O. simia)* have an increased suitable habitat area, while *O. militaris* has a decreased suitable habitat area[8]. In northern China, a representative species of temperate terrestrial orchids, *Cypripedium macranthos*, is expected to have an increased suitable habitat area in the future[9]. Under future climate, *Dendrobium moniliforme* is predicted to have an increased suitable habitat area, while *D. nobile* is expected to have a decreased suitable habitat area. However, climate change has a relatively small impact on their distribution in Japan and Korea[10].

Changnienia amoena, belonging to the Orchidaceae family, subtribe Calypsoinae, and the monotypic genus *Changnienia*, is a terrestrial orchid endemic to China. It is primarily distributed in the central and eastern China, at altitudes ranging from 400 to 1700 m in the mid-subtropical hilly and mountainous areas[11]. *C. amoena* is

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characterized by having only a single leaf and a single flower, with a large and vibrant purplish-pink flower[12] that is bilaterally symmetrical, making it highly ornamental. The entire plant has medicinal properties for treating coughs, while its pseudobulb is used for treating eczema, ulcers, scabies, and poisonous snake bites[13]. Due to structural defects in its flowers, *C. amoena* relies exclusively on bumblebees (*Bombus*) for pollination under natural conditions, utilizing a deceptive pollination mechanism, where no rewards are offered to the pollinators. As a result, its natural fruit set rate is low[14]. *C. amoena* can only reproduce through limited asexual propagation via pseudobulbs[15]. Additionally, excessive human harvesting and habitat fragmentation have severely depleted wild populations of *C. amoena*, leading to its classification as a nationally Class II protected species in China (https://www.forestry.gov.cn/main/3457/20210915/143259505655181.html). It was assessed as Endangered (EN) by the International Union for Conservation of Nature (IUCN) in 2004 (https://www.iucnredlist.org/search). *C. amoena* is considered a more primitive type within the tribe Epidendreae[16]. It has a narrow suitable range and stringent habitat requirements[17]. Currently, there is still a lack of understanding regarding the potential suitable areas for *C. amoena* and their distribution patterns and conservation strategies in response to future climate change.

The concept of ecological niche was first proposed by Grinnell[18,19], describing the functional role of a species within an ecosystem and its interactions with the environment and other species[20]. Species distribution refers to the range and patterns of a species' presence in geographic space. Species Distribution Models (SDMs), as well as Ecological Niche Models (ENMs), integrate species occurrence records with corresponding environmental data to estimate a species' niche requirements. These models connect the potential niche (PN) with the realized niche (RN) to explore the distribution patterns of species across different geographic regions[20]. Commonly used SDMs include the generalized linear model (GLM)[21], the Bioclimate analysis and prediction system model (BIOCLIM)[22], the Random Forest model (RF)[23], the Maximum Entropy Model (MaxEnt)[24], and the Ecological Niche Factor Analysis model (ENFA)[25]. Among them, the presence-only species distribution models-the Maximum Entropy Model (MaxEnt) is a machine learning model that uses presence and background data. Due to its simplicity, high predictive accuracy, and minimal requirement for species occurrence data, MaxEnt has been widely applied in assessing the distribution and habitat suitability of rare and endangered plants[26–32]. Numerous studies have demonstrated that MaxEnt, as a presence-only method, can produce robust species distribution evaluations comparable to those generated by presence-absence methods[33–35].

In this study, we used the MaxEnt model to simulate and predict potential suitable areas, exploring the potential distribution and migration patterns of *C. amoena* in China under different timeframes (2050s and 2090s) and emission scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5). The aim is to provide a scientific basis for in-situ conservation, ex-situ conservation, cultivation, and resource utilization of *C. amoena* wild resources.

Results

Model accuracy and dominant environmental variables

After removing environmental variables with correlation coefficients greater than |0.8|, a total of 19 environmental variables were selected for MaxEnt model prediction (Fig. 1; Table 1). The predictive accuracy of the model was assessed through AUC and CBI metrics, with the training set demonstrating a mean AUC of 0.990 and CBI of 0.959. This indicates extremely high model accuracy, making it suitable for predicting the potential distribution areas of *Changnienia amoena*.

The contribution rates of the eight environmental variables affecting the distribution of *C. amoena* are as follows: min temperature of coldest month (Bio06) at 26.1%, annual precipitation (Bio12) at 19.4%, isothermality (Bio03) at 13.5%, land use classification at 9.4%, slope at 6%, topsoil USDA texture classification at 4.7%, elevation at 4.7%, and topsoil calcium carbonate at 4%. Together, these variables account for a cumulative contribution of 87.8%[36,37], making them the dominant environmental variables influencing the distribution of *C. amoena*.

The optimal environmental variable combinations for the suitable growth of *C. amoena* are as follows: min temperature of coldest month (Bio06) between −5.8 and −0.36 °C, annual precipitation (Bio12) ranging from 749 to 3331.91 mm, isothermality (Bio03) between 22.9 and 28.6%, land use classification as forest land, slope > 0.975, topsoil USDA texture classification as silty clay, silt, and loam, elevation ranging from 384.11 to 1963.01 m, and topsoil calcium carbonate < 0.05%.

Current and future potential distribution areas of *Changnienia amoena*

The MaxEnt model was used to predict the distribution areas of *C. amoena* (Fig. 2). Based on the reclassification (MTSS = 0.1876), the areas of each suitability level were obtained (Table 2), and the distribution of each suitability level in various provinces was analyzed (Fig. 3).

Under the current climate scenario, the total area of suitable habitat for *C. amoena* is 36.64×10^4 km^2, with the primary concentrations in the provinces of Hubei, Shaanxi, Hunan, Chongqing, Sichuan, Zhejiang, Guizhou, and Anhui. The area of highly suitable habitat is 7.31×10^4 km^2, accounting for 19.95% of the total suitable distribution area. High suitability habitat is primarily found Dalou Mountain, Wu Mountain, Shennongjia Mountain in the northwest of Hubei, Wuling Mountain, Xuefeng Mountain in northern Hunan, Fangdou Mountain in southeastern Chongqing, Daba in northern Sichuan and southern Shaanxi's, Dabie Mountain in Anhui, and sporadically Tianmu Mountain, Tiantai Mountain, Siming Mountain in Zhejiang, and Wugong Mountain in Jiangxi.

The area of moderately suitable habitat is 9.16×10^4 km^2, representing 25% of the total suitable distribution area, and is mainly distributed around the highly suitable habitats. The area of low suitability habitat is 20.17×10^4 km^2, accounting for 55.05% of the total suitable distribution area. Besides the edges of highly and moderately suitable habitats, low suitability areas are also found in Shandong, Henan, Guangxi, Yunnan, Tibet, Fujian, and Liaoning.

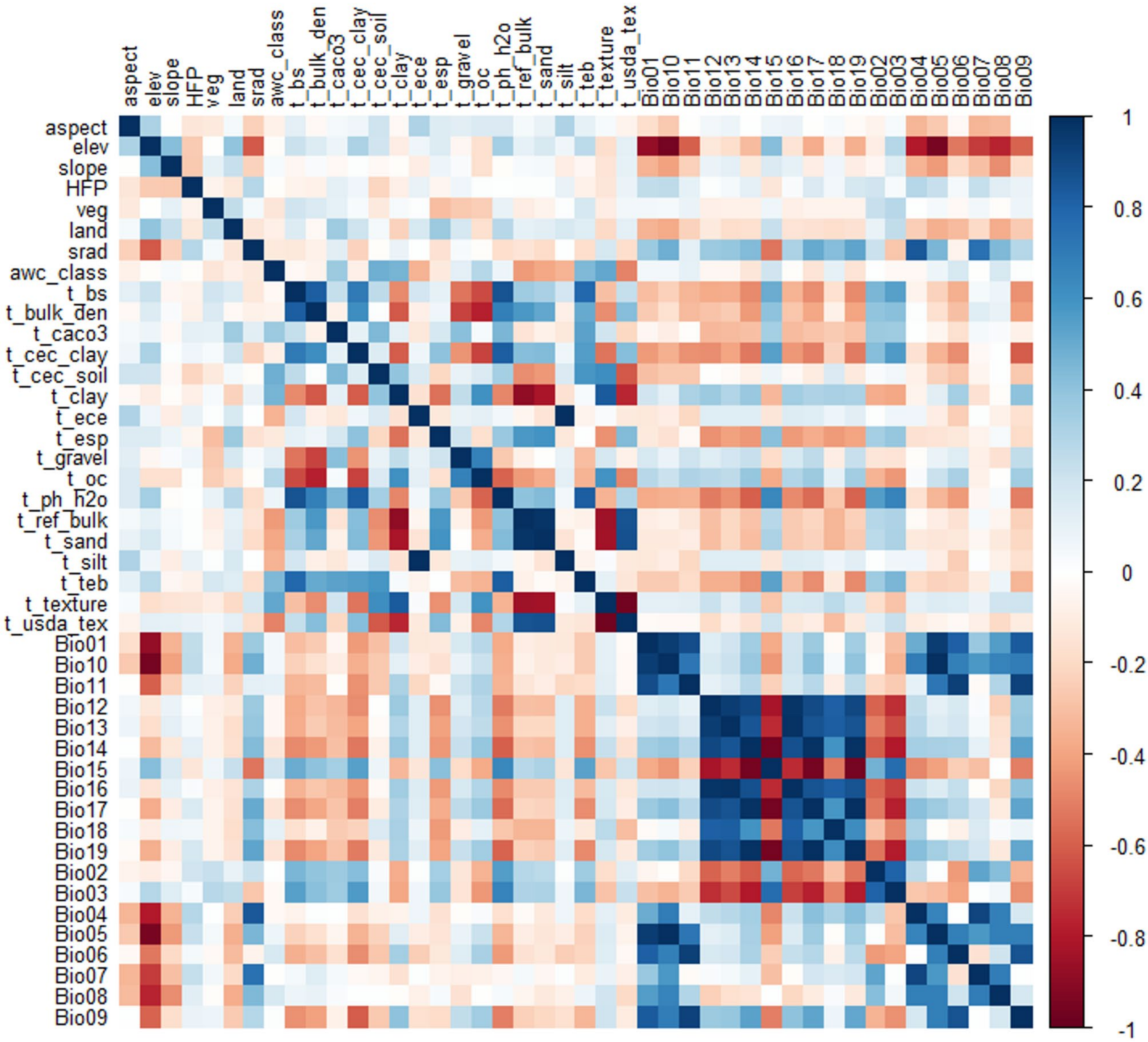

Fig. 1. Spearman correlation coefficients between the environmental variables.

Spatial pattern changes in future

Under a low greenhouse gas emission scenario (SSP1-2.6), the predicted suitable habitat for *C. amoena* is expected to extend northwest compared to the current climate. By the 2050s and 2090s, the total suitable habitat area is projected to slightly decrease, with areas of 34.87×10^4 km^2 and 34.96×10^4 km^2, respectively, showing reductions of 4.82% and 4.57%. These suitable habitats are primarily located in Shaanxi, Hubei, Sichuan, Chongqing, Xinjiang, Hunan, Henan, Shandong, Zhejiang, Jiangsu, and Jiangxi. By the 2050s, highly suitable habitats are estimated to cover 7.18×10^4 km^2, concentrated in northwestern Hubei, southern Shaanxi, Chongqing, and Anhui. Moderately suitable habitats will cover 7.37×10^4 km^2, mainly surrounding the highly suitable areas, while low suitability habitats will increase to 20.33×10^4 km^2, with notable increases in Xinjiang, Liaoning, and Shandong. By the 2090s, the areas of highly, moderately, and lowly suitable habitats are expected to be 20.94×10^4 km^2, 7.29×10^4 km^2, and 6.73×10^4 km^2, respectively, with distribution patterns similar to those in the 2050s.

Under a moderate greenhouse gas emission scenario (SSP2-4.5), the predicted suitable habitat for *C. amoena* will significantly extend northwest compared to the current climate. By the 2050s, the total suitable habitat area is projected to increase to 38.21×10^4 km^2, a 4.27% rise from the current distribution. The suitability levels are expected to be: low suitability at 23.21×10^4 km^2 (60.74%), moderately suitable at 7.72×10^4 km^2 (20.19%), and highly suitable at 7.28×10^4 km^2 (19.06%). By the 2090s, the suitable habitat area is forecasted to rise to 53.14×10^4 km^2, a 45.04% increase from the current climate. The distribution will include 38.02×10^4 km^2 (71.54%) of low suitability, 8.35×10^4 km^2 (15.71%) of moderately suitable, and 6.78×10^4 km^2 (12.76%) of highly suitable habitats.

Code	Environmental variables	Contribution (%)	Unit	Optimal range of variation	Highest optimal value
Bio06	Min Temperature of Coldest Month	26.1	°C	-5.8-0.36	-2.53
Bio12	Annual Precipitation	19.4	mm	749-3331.91	1461.51
Bio03	Isothermality	13.5	%	22.9–28.6	26.8
land	Land Use Classification	9.4	name	2[a]	2
slope	Slope	6	°	> 0.975	2.75
t_usda_tex	Topsoi1 USDA Texture Classification	4.7	name	2, 6, 9[b]	9
elev	Elevation	4.7	m	384.11-1963.01	706.18
t_caco3	Topsoil Calcium Carbonate	4	%	<-0.05	< 0.17
t_bs	Topsoil Base Saturation	3.6	%	8.6-47.24, 85.28–93.56	91.52
veg	Vegetation	2.7	Name	1, 3, 4[c]	3
srad	Solar Radiation	1.8	$kJ\cdot m^{-2}\cdot day^{-1}$	< 14366.67	12611.64
awc_class	Soil Available Water Content	0.9	name	1[d]	1
aspect	Aspect	0.8	°	> 20.5	326.33
t_gravel	Topsoil Gravel Content	0.7	%	2.8–8.72	3.56
HFP	Human Footprint	0.6	-	13.69–44.49	20.61
Bio08	Mean Temperature of Wettest Quarter	0.5	°C	16.65–25.09	20.43
t_oc	Topsoil Organic Carbon (% weight)	0.3	%	0.55–1.36	0.79
t_esp	Topsoil Sodicity (ESP)	0.2	%	0.26–1.64	0.66
t_ece	Topsoil Salinity (Elco)	0.1	dS/m	19.55–38.60	36.46

Table 1. Contribution of environmental variables and optimal growth values for *Changnienia amoena*. Note: [a] 2. forest land; [b] 2. silty clay, 6. silt, 9. loam; [c] 1. coniferous forest, 3. broadleaf forest; 4. shrub land; [d] 1. 150 mm/m.

Under a high greenhouse gas emission scenario (SSP5-8.5), the suitable habitat range for *C. amoena* will greatly extend northwest compared to the current climate, with an increase in the total suitable habitat area. By the 2050s, the total suitable habitat is predicted to reach 46.42×10^4 km^2, a 26.7% increase from the present. The habitat suitability levels are expected to be: low suitability at 30.81×10^4 km^2 (66.36%), moderately suitable at 8.10×10^4 km^2 (17.45%), and highly suitable at 7.52×10^4 km^2 (16.19%). By the 2090s, the total suitable habitat area is projected to expand to 109.21×10^4 km^2, an increase of 198.08% from the current climate. The distribution will include 72.32×10^4 km^2 (66.22%) of low suitability, 26.01×10^4 km^2 (23.81%) of moderately suitable, and 10.89×10^4 km^2 (9.97%) of highly suitable habitats.

Overall, under both SSP2-4.5 and SSP5-8.5 scenarios, the total area of suitable habitat for *C. amoena* is expected to increase. In the SSP2-4.5 scenario, the increase is primarily in low-suitability habitats in Xinjiang and Liaoning, while moderately and highly suitable habitats in Zhejiang, Anhui, Hunan, and Chongqing will decrease compared to the current climate. In the SSP5-8.5 scenario, all levels of suitability will see increases, with the most significant growth in low-suitability habitats, mainly in high-latitude regions such as Xinjiang, Inner Mongolia, Liaoning, and Gansu (Fig. 4).

Changnienia amoena centroid migration

The centroid of the modern suitable habitat for *C. amoena* is located in Changyang County, Yichang City, Hubei Province (111.027°E, 30.623°N), at an elevation of 671 m. As the climate warms, the centroid of the suitable habitat for *C. amoena* is expected to gradually shift northwest to adapt to future weather changes. The extent of this migration is related to carbon emission scenarios: higher carbon emissions led to stronger warming and greater migration distances.

Under the SSP1-2.6 scenario, by the 2050s, the centroid is projected to migrate 274.32 km northwest to near Wudang Mountain in Xunyang County, Ankang, Shaanxi Province (109.574°E, 32.758°N), at an elevation of 907 m. By the 2090s, it will continue to move 85.12 km northwest to Hanbin District, Ankang, Shaanxi Province (108.794°E, 33.155°N), at an elevation of 1336 m.

Under the SSP2-4.5 scenario, the centroid will migrate 398.87 km northwest to Xixiang County, Hanzhong, Shaanxi Province (108.049°E, 33.168°N), at an elevation of 839 m by the 2050s, and further 628.69 km to Huahong County, Haidong, Qinghai Province (102.192°E, 36.129°N), at an elevation of 2947 m by the 2090s.

Under the SSP5-8.5 scenario, the centroid will move 756.11 km northwest to Zhangxian County, Dingxi, Gansu Province (104.553°E, 34.693°N), at an elevation of 2076 m by the 2050s, and an additional 779.89 km to Su'nan County, Zhangye, Gansu Province (98.168°E, 39.521°N), at an elevation of 3154 m by the 2090s (Fig. 5).

Discussion

This study utilized the MaxEnt model to predict the current and future potential suitable habitats for *Changnienia amoena*. The model demonstrated exceptional predictive performance, achieving an AUC of 0.990 and a CBI of 0.959. The current actual distribution of *C. amoena* is largely within the predicted potential distribution areas, suggesting that the predictions are reliable. Although the species has a broad distribution range, the number of wild individuals is low, and the habitat is highly fragmented. Recently, new distribution points for *C. amoena*

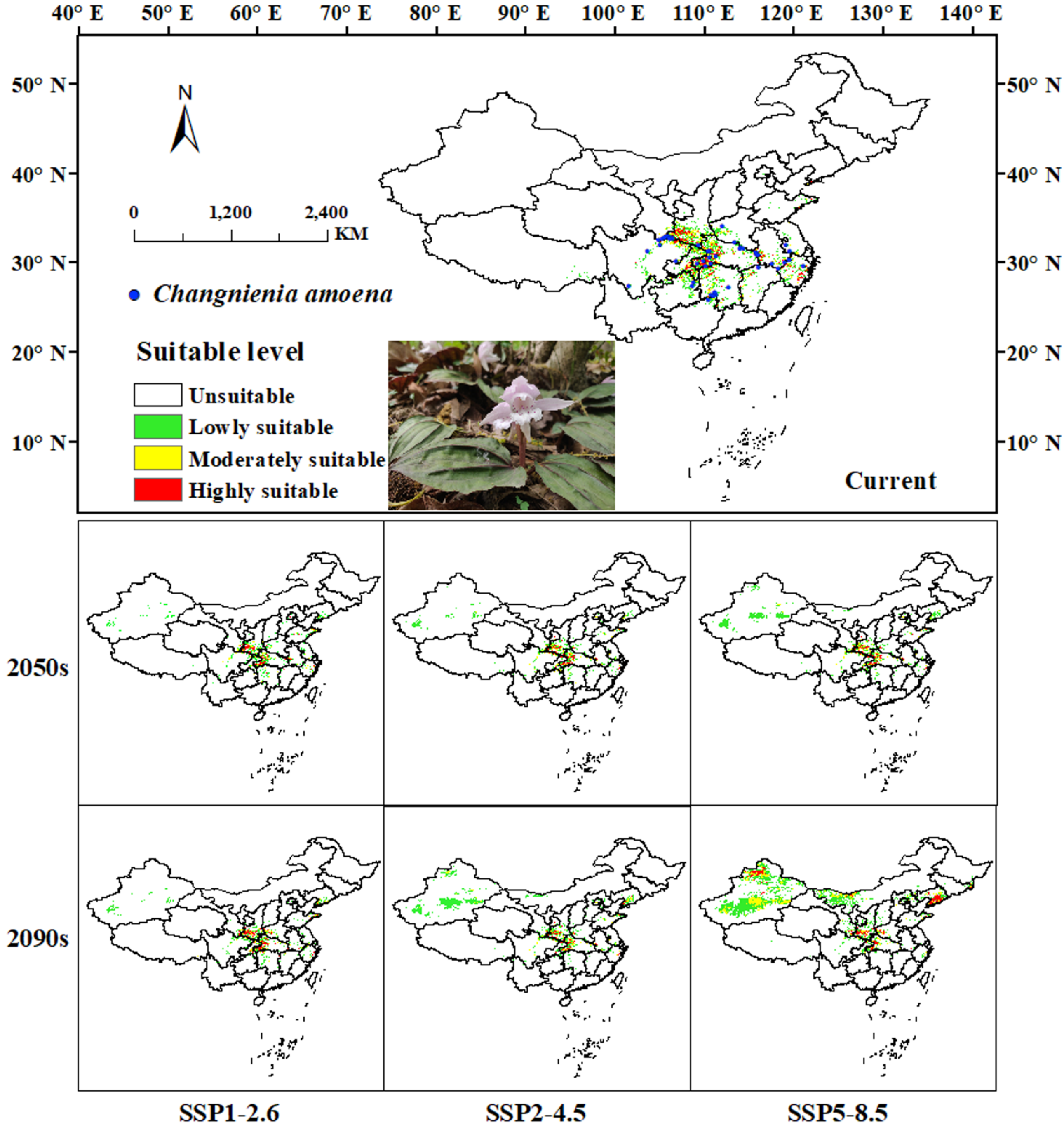

Fig. 2. Distribution of potential suitable habitat for *Changnienia amoena* under current and future climate models. The map was generated using ArcGIS 10.8.1 (Esri, Redlands, CA, USA).

have been reported, including locations such as Wenxian in Gansu[38], Fanjing Mountain in Guizhou[39], Mao'er Mountain in Guangxi[40], and Liyang in Jiangsu (http://lyj.jiangsu.gov.cn/art/2023/4/10/art_7147_10857763.html). This suggests that there may be many undiscovered new distribution records. Based on the MaxEnt model's predictions, potential distribution areas include regions that have not been previously recorded, such as Henan, Shandong, Tibet, and Yunnan, indicating that the actual distribution might be broader than currently observed. This calls for detailed field surveys in these areas to uncover additional new distribution points for *C. amoena*.

The cumulative contribution value of the eight environmental factors, including the minimum temperature of the coldest month (Bio06), annual precipitation (Bio12), isothermality (Bio03), land use classification, slope, topsoil USDA texture classification, elevation, and topsoil calcium carbonate, exceeds 85%, making them the dominant environmental variables influencing the distribution of *C. amoena*. Similar to other orchid species[41], the distribution of *C. amoena* is jointly constrained by temperature, precipitation, land use, topography, and soil characteristics, indicating that orchids have relatively stringent habitat requirements. Particularly, temperature

Periods	Lowly suitable	Moderately suitable	Highly suitable	Total	Expansion	Unchanged	Contraction
Current	20.17	9.16	7.31	36.64			
2050s	SSP1-2.6 20.33	7.37	7.18	34.87	8.71	26.17	10.48
	SSP2-4.5 23.21	7.72	7.28	38.21	10.85	27.36	9.28
	SSP5-8.5 30.81	8.10	7.52	46.42	20.60	25.82	10.82
2090s	SSP1-2.6 20.94	7.29	6.73	34.96	10.31	24.66	11.99
	SSP2-4.5 38.02	8.35	6.78	53.14	30.22	22.92	13.72
	SSP5-8.5 72.32	26.01	10.89	109.21	91.98	17.23	19.41

Table 2. Dynamic changes of suitable areas of *Changnienia amoena* under different climate scenarios ($\times 10^4$ km^2).

(Bio06 and Bio03) and precipitation (Bio12) have a more significant impact on the distribution of *C. amoena* compared to land use classification, topography, and soil characteristics, with temperature contributing 39.6% and precipitation 19.4%. An analysis of the optimal environmental factors reveals that *C. amoena* thrives under specific conditions, including a minimum temperature of the coldest month (Bio06) ranging from − 5.8 to -0.36 °C, annual precipitation (Bio12) between 749 and 3331.91 mm, and isothermality (Bio03) between 22.9% and 28.6%. Additionally, it is typically found in forested areas with slopes greater than 0.975, topsoil classified as silty clay, silt, or loam according to the USDA texture classification, elevations ranging from 384.11 to 1963.01 m, and topsoil calcium carbonate content below 0.05%. These conditions suggest that *C. amoena* flourishes in environments with relatively mild winter temperatures, abundant rainfall, stable and warm climatic conditions, and well-aerated clay soils at medium to low elevations. This aligns with field observations, which indicate that *C. amoena* is commonly found in moist habitats with sufficient soil moisture[42] and good drainage[14].

Under the SSP1-2.6 scenario, the suitable habitat area for *C. amoena* slightly contracts. In contrast, under the SSP2-4.5 and SSP5-8.5 pathways, the suitable habitat area decreases in lower-latitude regions but increases significantly in higher-latitude regions, with the expansion significantly exceeding the area loss. This suggests that the increase in CO_2 concentration may promote the expansion of *C. amoena* populations. In the future, new suitable habitats for *C. amoena* are expected to emerge significantly in higher-latitude regions of northwestern China, such as Xinjiang and Inner Mongolia. This may be related to the warming and increased precipitation trends in northwestern China as the region shifts towards a "warming and wetting" climate due to global warming[43,44]. This phenomenon reflects the adaptive evolution of *C. amoena* to future climate conditions. Likewise, the mountainous regions of southwest China are expected to act as refugia for *Habenaria* and *Calanthe* species of Orchidaceae under future climate scenarios[7]. The trend of plant migration toward higher latitudes and elevations under future climate change has also been observed in other studies, yielding similar results for species such as *Tetracentron sinense*[28], *Thuja koraiensis*[45], *Acer truncatum*[46], and so on, encompassing a total of 125 plant species distributed across China[47].

Changnienia amoena is a monotypic genus species with highly fragmented habitats and significantly genetic differentiated populations, making it migration difficult[48]. As a result, the species is more susceptible to climate change and may even face the risk of extinction. Northern and northwestern China, including regions like Xinjiang, Inner Mongolia, and Liaoning, could become potential new habitats for *C. amoena* in the future. It is important to plan spatially in these areas to ensure sufficient space for *C. amoena* and to consider conducting introduction and cultivation experiments when necessary. As the suitable habitat area for *C. amoena* expands, constructing corridors to connect different populations and enhance gene flow between them could be considered. In Hubei and Shaanxi, where *C. amoena* populations are stable, the efficiency of in-situ conservation efforts should be strengthened. In the southern edge regions of *C. amoena*, such as Zhejiang, Anhui, Hunan, Guangxi, and Sichuan, the habitat area is expected to continue to decrease, so monitoring in these areas should be enhanced, and *ex-situ* conservation efforts should be prioritized.

However, our study has limitations. While we predict that the potential niche of *C. amoena* may be broader than its realized niche due to the exclusion of certain key biological factors, such as symbiotic mycorrhizae, specific pollinators and their dispersal ability, and interspecific competition[49]. These factors play a crucial role in limiting the actual distribution of *C. amoena*. For example, symbiotic mycorrhizae may affect its establishment success, while the absence of specific pollinators may constrain its reproduction. Additionally, interspecific competition may further reduce the range of suitable habitats. Therefore, our predictions may overestimate its potential niche, while the realized niche is likely more constrained by biotic interactions. Furthermore, our study relies on a single future climate model and assumes that ecological factors beyond bioclimate will remain constant under future climate scenarios. To improve the accuracy of future predictions, comparative analyses using multiple climate models should be conducted, and efforts should be made to collect more precise and up-to-date data, incorporating these factors into future research. This would contribute to a more comprehensive understanding of the distribution dynamics of *C. amoena*.

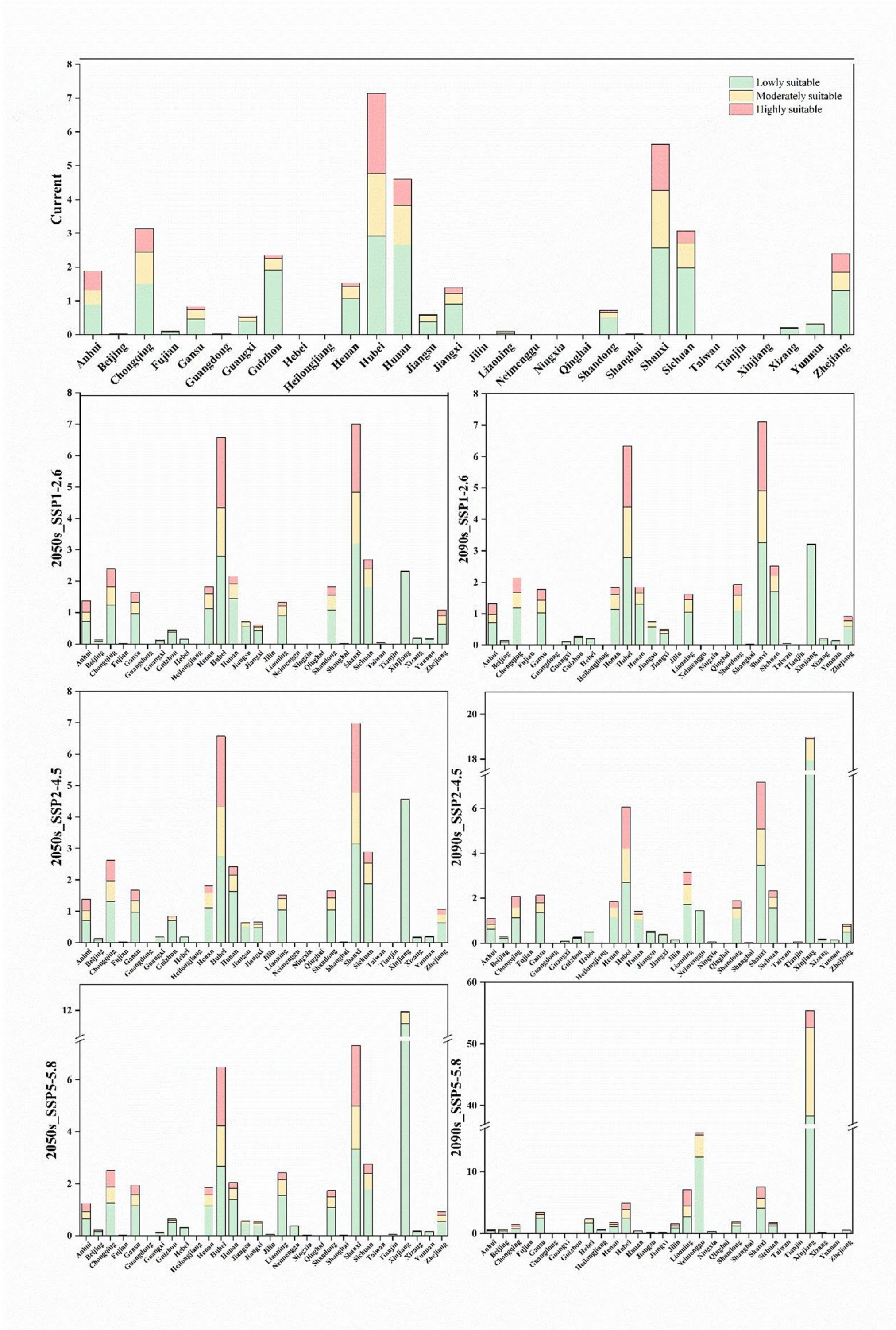

Fig. 3. Area of suitable habitat for *Changnienia amoena* under current and future climate models by province in China.

Methods

Distribution records and processing

A total of 80 distribution records of *Changnienia amoena* were obtained by searching through digital platforms, including the Global Biodiversity Information Facility (GBIF, http://www.gbif.org), the Chinese Virtual Herbarium (CVH, http://www.cvh.org.cn), the Teaching Specimen Resource Sharing Platform (http://mnh.scu.edu.cn/main.aspx), the National Specimen Information Infrastructure (NSII, http://www.nsii.org.cn/2017/ho

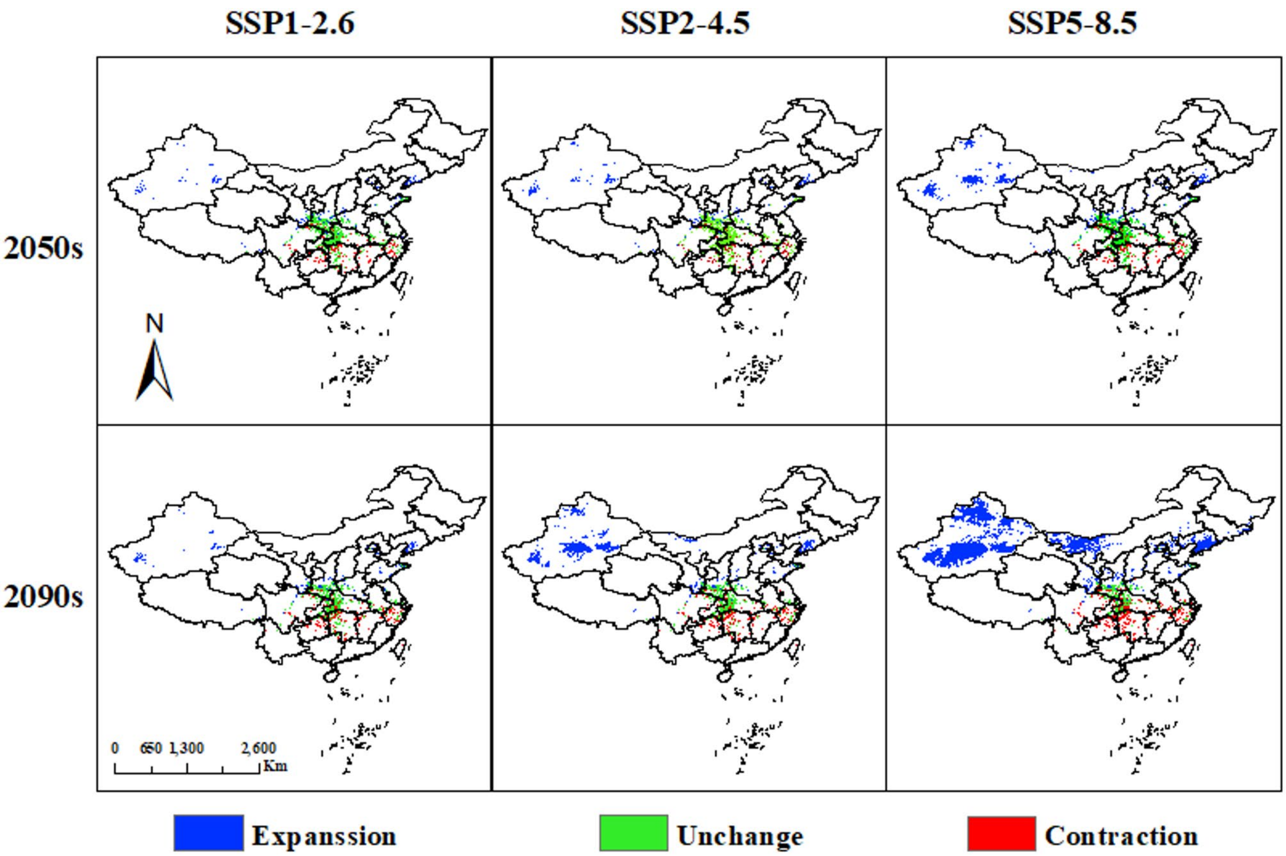

Fig. 4. Spatial changes in suitable habitats for *Changnienia amoena*. The map was created using ArcGIS 10.8.1 (Esri, Redlands, CA, USA).

me.php), and the Chinese Plant Image Database (PPBC, https://ppbc.iplant.cn), in combination with literature data and field survey data. All the specimens were identified by Xingjian Liu from the Herbarium of Jiangsu Institute of Botany, Chinese Academy of Sciences. Records of artificially introduced and cultivated specimens, as well as duplicate distribution records, were excluded. To reduce sampling bias, the "Dismo" package[50] in R was used to remove closely located distribution points, retaining only one distribution point per 1 km x 1 km grid. This resulted in 48 valid distribution records, which were used for model simulation.

Selection of environmental variables

Modern and future data for 19 bioclimatic variables, solar radiation, and elevation were obtained from the WorldClim database (http://www.worldclim.org). Eighteen topsoil characteristics were sourced from the Harmonized World Soil Database[51]. Human footprint (HFP) data were acquired from the Center for International Earth Science Information Network (CIESIN) and the Socioeconomic Data and Applications Center (SEDAC)[52]. Slope and aspect were derived from the Digital Elevation Model (DEM), while vegetation types, and land use classification were obtained from the National Fundamental Geographic Information System (http://nfgis.nsdi.gov.cn). Basemap of China was sourced from the Resource and Environment Science Data Platform (https://www.resdc.cn/DOI/)[53]. All environmental variables had a spatial resolution of 30 arc-s econds (Table 3). Then, variable processing and spatial mapping were performed using ArcGIS 10.8.1 (Esri, Redlands, CA, USA). The ACCESS-CM2 model is selected for future climate modeling, as it demonstrates relatively outstanding performance in simulating future temperature and precipitation patterns in China[54]. Future climate variables were based on the climate change scenarios from the IPCC (Intergovernmental Panel on Climate Change) sixth assessment report, known as shared socioeconomic pathways (SSPs)[55]. Two periods were selected: the 2050s (representing 2041–2060) and the 2090s (representing 2081–2100). These periods include three greenhouse gas emission scenarios: SSP1-2.6, SSP2-4.5, and SSP5-8.5, representing low, medium, and high emission scenarios, respectively, with a focus on sustainable development for the lowest emissions. Except for bioclimatic variables, other environmental variables were assumed to remain unchanged in the future. To avoid the impact of correlations among the 44 environmental variables on the predictive accuracy of the model, Spearman correlation coefficients between the environmental variables were assessed using the "corrplot" package[56] in R for variables with a correlation coefficient greater than |0.8|, only those with higher contribution values were retained for predicting the potential suitable habitat of *C. amoena*.

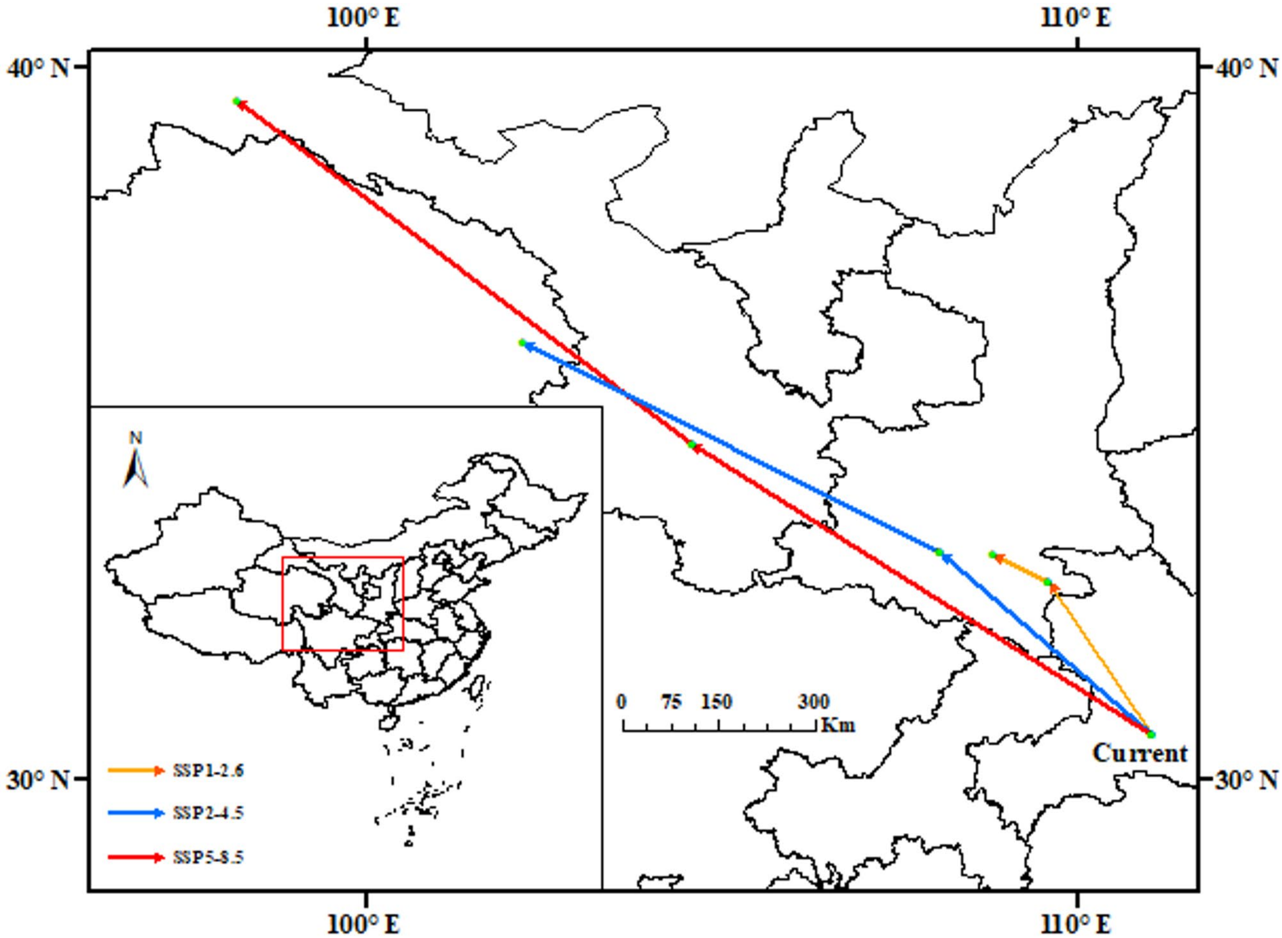

Fig. 5. Centroid migration for *Changnienia amoena*. The map was produced using ArcGIS 10.8.1 (Esri, Redlands, CA, USA).

MaxEnt modeling

MaxEnt version 3.4.1[57] was used to predict the potential distribution of *C. amoena* under current and future periods. The parameters were set as follows: the maximum number of background points is set to 10,000. 25% of the sample data was randomly selected for model testing, while the remaining 75% was used for model training. The model was run 10 times with random seeds, using 500 bootstrap replications, the output is chosen as cloglog (complementary log-log), which is considered to offer a stronger theoretical justification compared to the conventional logistic transform[58], and other settings were kept as default. After the model operation was completed, the accuracy of the model predictions was evaluated using the area under the receiver operating characteristic curve (AUC) and continuous Boyce Index (CBI), respectively. The AUC value ranges from 0 to 1, with values closer to 1 indicating higher predictive accuracy. Specifically, an AUC value of 0.9–1.0 indicates very high model accuracy, 0.8–0.9 indicates high accuracy, 0.6–0.7 indicates poor accuracy, and values below 0.6 indicate model failure[59]. The CBI value ranges from − 1 to 1, with values closer to 1 indicating stronger predictive ability of the model[60,61]. The Jackknife method was used to evaluate the contribution of each environmental variable to the model. The importance of environmental variables in the model simulation was analyzed using the contribution rates generated by the MaxEnt model, and the value ranges of each variable were extracted to analyze the suitable ecological niche parameters for *C. amoena* under current climatic conditions.

Habitat suitability classification

The maximum training sensitivity plus specificity cloglog threshold (MTSS) was used to classify the habitat suitability for *C. amoena*[62]. The potential distribution areas were reclassified into four suitability levels as follows: areas with suitability < MTSS were considered unsuitable; MTSS – 0.4 were classified as low suitability; 0.4–0.6 as medium suitability; and > 0.6 as high suitability. The total area of each suitability category was calculated, as well as the area of each category within different provinces in China.

Distribution pattern changes

Using MTSS as the threshold, *C. amoena* was converted into binary files representing suitable and unsuitable areas. The SDMtoolbox v2.6[63] was used for overlay analysis to visualize the contraction and expansion of suitable distribution areas under different future scenarios compared to the current distribution. Additionally, centroid

Type	Code	Environmental variables
	Bio01	Annual Mean Temperature
	Bio02	Mean Diurnal Range
	Bio03	Isothermality (Bio2 / Bio7) (×100)
	Bio04	Temperature Seasonality
	Bio05	Max Temperature of the Warmest Month
	Bio06	Min Temperature of Coldest Month
	Bio07	Temperature Annual Range (Bio5-Bio6)
	Bio08	Mean Temperature of Wettest Quarter
	Bio09	Mean Temperature of Driest Quarter
Bioclimate	Bio10	Mean Temperature of Warmest Quarter
	Bio11	Mean Temperature of Coldest Quarter
	Bio12	Annual Precipitation
	Bio13	Precipitation of Wettest Month
	Bio14	Precipitation of Driest Month
	Bio15	Precipitation Seasonality (Coefficient of Variation)
	Bio16	Precipitation of Wettest Quarter
	Bio17	Precipitation of Driest Quarter
	Bio18	Precipitation of Warmest Quarter
	Bio19	Precipitation of Coldest Quarter
	aspect	Aspect
Terrain	elve	Elevation
	slope	Slope
	awc_class	Soil Available Water Content
	t_clay	Percentage of Clay in the Topsoil
	t_oc	Topsoil Organic Carbon (% weight)
	t_ph_h2o	Topsoil pH (H_2O) (-log(H+))
	t_ref_bulk	Topsoil Refernce Bulk
	t_sand	Topsoil Sand Fraction (% wt)
	t_silt	Percentage of Silt in the Topsoil
	t_texure	Topsoil Texure
Soil	t_gravel	Topsoil Gravel Content
	t_usda_tex	Topsoi1 USDA Texure Classification
	t_cec_clay	Topsoi1 CEC (clay)
	t_bs	Topsoil Base Saturation
	t_teb	Topsoi1 TEB
	t_caco3	Topsoil Calcium Carbonate
	t_esp	Topsoil Sodicity (ESP)
	t_ece	Topsoil Salinity (Elco)
	t_bulk_den	Topsoil Reference Bulk Density
	HFP	Human Footprint
	solar	Solar Radiation
Others	veg	Vegetation
	land	Land Use Classification

Table 3. The environmental variables for MaxEnt modeling.

migration trends were analyzed to determine the changes in the distribution patterns of suitable areas for *C. amoena*.

Conclusions

This study systematically explored the influence of environmental variables on *Changnienia amoena* and the current potential suitable habitats as well as future spatial pattern changes by integrating bioclimatic, topographic, soil, land use, vegetation type, and human footprint variables. The conclusions are as follows: (1) The actual current distribution of *C. amoena* largely falls within its potential distribution area, and the potential distribution area might be broader than the observed range, suggesting the possibility of discovering new distribution points for *C. amoena*. (2) The eight environmental variables, including the minimum temperature of coldest month (Bio06), annual precipitation (Bio12), isothermality (Bio03), land use classification, slope, topsoil USDA texture classification, elevation, and topsoil calcium carbonate, are the dominant variables influencing the distribution of *C. amoena*. (3) Under the future SSP1-2.6 scenario, the suitable habitat area for *C. amoena* slightly decreased. In contrast, under the SSP2-4.5 and SSP5-8.5 scenarios, the suitable habitat area decreases in lower-latitude regions but increases in higher-latitude regions, with the expansion significantly exceeding the area loss. Finally, based on the prediction results, the following conservation recommendations are proposed for *C. amoena*: it is recommended to conduct pre-emptive introduction and cultivation experiments in regions projected to become suitable for expansion. Additionally, building corridors to connect different populations can enhance genetic exchange. Efforts should also focus on improving the efficiency of in-situ conservation in stable distribution areas, while strengthening monitoring in regions where the distribution is anticipated to decline. In such areas, measures like artificial pollination and prioritizing ex-situ conservation efforts should be implemented.

Data availability

The authors confirm that the data supporting the findings of this study are available within the article, and further requests can be directed to the corresponding author.

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References

1. IPCC. *Climate Change 2021: The Physical Science Basis* (Cambridge University Press, 2021).
2. Monastersky, R. Global carbon dioxide levels near worrisome milestone. *Nature* **497**, 13–14 (2013).
3. Cribb, P. J. Genera Orchidacearum. in Orchidaceae (eds Pridgeon, A. M., Cribb, P. & Chase, M. W.) (Oxford University Press, (2001).
4. Kolanowska, M., Michalska, E. & Konowalik, K. The impact of global warming on the niches and pollinator availability of sexually deceptive Orchid with a single pollen vector. *Sci. Total Environ.* **795**, 148850 (2021).
5. Swarts, N. D. & Dixon, K. W. Terrestrial Orchid conservation in the age of extinction. *Ann. Botany*. **104**, 543–556 (2009).
6. Kirillova, I. A., Dubrovskiy, Y. A., Degteva, S. V. & Novakovskiy, A. B. Ecological and habitat ranges of orchids in the northernmost regions of their distribution areas: A case study from ural mountains, Russia. *Plant. Divers.* **45**, 211–218 (2023).
7. Qiu, L. et al. Contrasting range changes of terrestrial orchids under future climate change in China. *Sci. Total Environ.* **895**, 165128 (2023).
8. Evans, A., Janssens, S. & Jacquemyn, H. Impact of climate change on the distribution of four closely related Orchis (Orchidaceae) species. *Diversity* **12**, 312 (2020).
9. Wu, Q. et al. Prediction of potential distribution of *Cypripedium macranthos* under climate change scenarios in China. *Acta Ecol. Sin.* **44**, 209–223 (2024).
10. Tang, X., Yuan, Y. & Zhang, J. How climate change will alter the distribution of suitable *Dendrobium* habitats. *Front. Ecol. Evol.* **8**, 536339 (2020).
11. Chen, X. Q., Cribb, P. J. & Gale, S. W. *Changnienia amoena*. in *Flora of China* (eds. Wu, Z. Y., Raven, P. H., Hong, D.Y.) Vol. 25 (Science Press and Missouri Botanical Garden Press, 2009).
12. Sun, H. Q., Alexandersson, R. & Ge, S. Positive effects of flower abundance and synchronous flowering on pollination success, and pollinia dispersal in rewardless *Changnienia amoena* (Orchidaceae). *Biol. J. Linn. Soc.* **99**, 477–488 (2010).
13. Jiang, W., Zhao, M. & Fu, C. Studies on in vitro regeneration competence of pseudobulb cultures in *Changnienia amoena* Chien. *Chin. Sci. Bull.* **56**, 2580–2585 (2011).
14. Sun, H., Luo, Y., Alexandersson, R. & Ge, S. Pollination biology of the deceptive Orchid *Changnienia amoena*. *Bot. J. Linn. Soc.* **150**, 165–175 (2006).
15. Sun, H. Morphological variation and its adaptive significance for *Changnienia amoena*, an endangered Orchid. *Biodivers. Sci.* **13**, 376 (2005).
16. Zhang, G. et al. Comprehensive phylogenetic analyses of Orchidaceae using nuclear genes and evolutionary insights into epiphytism. *JIPB* **65**, 1204–1225 (2023).
17. Li, X., Wang, Y. & Xu, M. Population size and habitat characteristics of *Changnienia amoena* S.S. Chien in Baohuashan nature reserve of Jiangsu Province. *Biotic Resour.* 467–471 (2022).
18. Grinnell, J. The niche-relationships of the California thrasher. *Auk* **34**, 427–433 (1917).
19. Grinnell, J. Presence and absence of animals. in *Joseph Grinnell's Philosophy of Nature* 195–216 (University of California Press, 1943).
20. Soberón, J. & Nakamura, M. Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 19644–19650 (2009).
21. Nelder, J. A. & Wedderburn, R. W. M. Generalized linear models. *J. R. Stat. Soc. Ser. (General)*. **135**, 370 (1972).
22. Wisz, M. S. et al. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **14**, 763–773 (2008).
23. Bar Massada, A., Syphard, A. D., Stewart, S. I. & Radeloff, V. C. Wildfire ignition-distribution modelling: a comparative study in the Huron–Manistee National forest, Michigan, USA. *Int. J. Wildland Fire*. **22**, 174 (2013).
24. Phillips, S. J. & Dudík, M. Modeling of species distributions with maxent: New extensions and a comprehensive evaluation. *Ecography* **31** (2008).
25. Hirzel, A. H., Hausser, J., Chessel, D. & Perrin, N. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* **83**, 2027–2036 (2002).
26. La Montagna, D. et al. Climate change effects on the potential distribution of the endemic *Commiphora* species (Burseraceae) on the Island of Socotra. *Front. Glob Change*. **6**, 1183858 (2023).
27. Lai, W. et al. Potential impacts of climate change on the distribution of the relict plant *Shaniodendron subaequale*. *Heliyon* **9**, e14402 (2023).
28. Gan, Y., Cheng, L., Tang, J., Han, H. & Gan, X. Evaluating the vulnerability of *Tetracentron sinense* habitats to climate-induced latitudinal shifts. *Ecol. Evol.* **14**, e11710 (2024).
29. Lawer, E. A. Predicting the impact of climate change on the potential distribution of a critically endangered avian scavenger, hooded Vulture Necrosyrtes Monachus, in Ghana. *Global Ecol. Conserv.* **49**, e02804 (2024).
30. Liu, Y., Wang, H., Yang, J., Dao, Z. & Sun, W. Conservation genetics and potential geographic distribution modeling of *Corybas taliensis*, a small 'sky Island' Orchid species in China. *BMC Plant. Biol.* **24**, 11 (2024).
31. Wang, Y. et al. Prediction of potential suitable habitats in the 21st century and GAP analysis of priority conservation areas of *Chionanthus retusus* based on the MaxEnt and Marxan models. *Front. Plant. Sci.* **15**, 1304121 (2024).
32. Wang, H., Zhi, F. & Zhang, G. Predicting impacts of climate change on suitable distribution of critically endangered tree species *Yulania zenii* (W. C. Cheng) D. L. Fu in China. *Forests* **15**, 883 (2024).
33. Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. & Kadmon, R. A comparative evaluation of presence-only methods for modelling species distribution. *Divers. Distrib.* **13**, 397–405 (2007).

34. Elith, J. & Leathwick, J. R. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697 (2009).
35. Gormley, A. M. et al. Using presence-only and presence–absence data to estimate the current and potential distributions of established invasive species. *J. Appl. Ecol.* **48**, 25–34 (2011).
36. Amat, M. E., Vargas, P. & Gómez, J. M. Effects of human activity on the distribution and abundance of an endangered mediterranean high-mountain plant (Erysimum penyalarense). *J. Nat. Conserv.* **21**, 262–271 (2013).
37. Yang, M. et al. Assessing risk from invasive alien plants in China: reconstructing invasion history and estimating distribution patterns of *Lolium temulentum* and *Aegilops tauschii*. *Front. Plant. Sci.* **14**, 1113567 (2023).
38. Zhang, H. New record of *Changnienia amoena* in Wen County, Gansu Province. *Plants* **29**, 29 (1996).
39. Zhang, Y. & Yang, C. New record of an Orchid species, *Changnienia amoena* (genus *Changnienia*), in Guizhou Province. *Seed* **29**, 65–66 (2010).
40. Qin, Y., Zou, C. & Meng, T. Two newly recorded genera of Orchidaceae from Guangxi, China. *Guihaia* **38**, 1475–1479 (2018).
41. Pica, A., Vela, D. & Magrini, S. Forest orchids under future climate scenarios: habitat suitability modelling to inform conservation strategies. *Plants* **13**, 1810 (2024).
42. Xiong, G., Xie, Z., Xiong, X., Fan, D. & Ge, S. The phenology, reproduction and community characteristics of *Changnienia amoena*, a rare species in Southern part of Shennongjia mountain range. *Acta Ecol. Sin.* **23**, 173–179 (2003).
43. Ding, Y. et al. Regional responses to global climate change: progress and prospects for trend, causes, and projection of Climatic warming-wetting in Northwest China. *Adv. Earth Sci.* **38**, 551–562 (2023).
44. Zhang, Q. et al. Climatic warming and humidification in the arid region of Northwest China: multi-scale characteristics and impacts on ecological vegetation. *J. Meteorological Res.* **35**, 113–127 (2021).
45. Yang, X. et al. Response to climate change and GAP analysis of *Thuja koraiensis* Nakai. *Plants* **13**, 1750 (2024).
46. Liu, Y. et al. Changes in potentially suitable areas for fruit utilization of *Acer truncatum* in China under climate change. *Forests* **15**, 713 (2024).
47. Wang, S. & Wu, J. Research progress on the changes in geographical distributions of plant species under future climate change scenarios in China. *Guihaia* (2024).
48. Li, A. & Ge, S. Genetic variation and conservation of *Changnienia amoena*, an endangered Orchid endemic to China. *Plant. Syst. Evol.* **258**, 251–260 (2006).
49. Laughlin, D. C. & McGill, B. J. Trees have overlapping potential niches that extend beyond their realized niches. *Science* **385**, 75–80 (2024).
50. Hijmans, R., Phillips, S., Leathwick, J. & Elith *J. Dismo: Species Distribution Model.* (2023).
51. Nachtergaele, F. O. & Verelst, L. W. D. Harmonized World Soil Database (2012).
52. Wildlife Conservation Society-WCS & Center For International Earth Science Information Network-CIESIN-Columbia University. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic) (NASA Socioeconomic Data and Applications Center (SEDAC), 2005). https://doi.org/10.7927/H4M61H5F
53. Xu, X. China's multi-year provincial administrative division boundary data. Environment Science and Data Registration and Publishing System (http://www.resdc.cn/DOI). https://doi.org/10.12078/2023010103 (2023).
54. Wang, M. & Li, Z. Future climate change prediction in Northeastern China based on CMIP6 multi-model. *Jilin Water Resour.* 1–10.
55. Moss, R. H. et al. The next generation of scenarios for climate change research and assessment. *Nature* **463**, 747–756 (2010).
56. Friendly, M. Corrgrams: exploratory displays for correlation matrices. *Am. Stat.* **56**, 316–324 (2002).
57. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259 (2006).
58. Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. & Blair, M. E. Opening the black box: an open-source release of maxent. *Ecography* **40**, 887–893 (2017).
59. Fielding, A. H. & Bell, J. F. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Envir Conserv.* **24**, 38–49 (1997).
60. Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. A. Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300 (2002).
61. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152 (2006).
62. Liu, C., White, M. & Newell, G. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* **40**, 778–789 (2013).
63. Brown, J. L., Bennett, J. R. & French, C. M. SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* **5**, e4095 (2017).

Author contributions

Conceptualization, X.L. and M.L.; methodology, X.L. and M.L.; software, T.L., Y.S. and M.L.; investigation, Q.S., J.S. and S.W.; data curation, T.L. and M.L.; writing—original draft preparation, M.L.; writing—review and editing, X.L. and M.L. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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