

Current distribution of two species of Chinese macaques (*Macaca arctoides* and *Macaca thibetana*) and the possible influence of climate change on future distribution

Wen-Bo Li^{1,2}  | Pei-Pei Yang² | Dong-Po Xia³  | Ming Li¹  | Jin-Hua Li^{2,4}

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

²International Collaborative Research Center for Huangshan Biodiversity and Tibetan Macaque Behavioral Ecology School of Resources and Environmental Engineering, Anhui University, Hefei, Anhui, China

³School of Life Sciences, Anhui University, Hefei, Anhui, China

⁴School of Life Sciences, Hefei Normal University, Hefei, Anhui, China

Correspondence

Ming Li, Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 100101, No. 5, Beichen Rd, Chaoyang District, Beijing, China.
Email: lim@ioz.ac.cn

Jin-Hua Li, International Collaborative Research Center for Huangshan Biodiversity and Tibetan Macaque Behavioral Ecology School of Resources and Environmental Engineering, Anhui University, 230601, No. 111, Jiulong Rd, Hefei, Anhui, China.
Email: jhli@ahu.edu.cn

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Abstract

Predicting the spatial distribution of species and suitable areas under global climate change could provide a reference for species conservation and long-term management strategies. *Macaca thibetana* and *Macaca arctoides* are two endangered species of Chinese macaques. However, limited information is available on their distribution, and their habitat needs lack proper assessment due to complicated taxonomy and less research attention. In recent years, scholars widely used the maximum entropy (MaxEnt) model to predict the impact of global climate and certain environmental factors on species distribution. Therefore, we used the MaxEnt model to predict the spatiotemporal distribution of both macaque species under six climate change scenarios using occurrence and high-resolution ecological data. We identified climatic factors, elevation, and land cover that shape their distribution range and determined shifts in their habitat range. The results demonstrated that temperature range, annual precipitation, forest land cover, and temperature seasonality, including the precipitation of the driest month are the main factors affecting their distribution. Currently, *M. thibetana* is mainly concentrated in central, eastern, southern, and southwestern China, and *M. arctoides* is mainly concentrated in three provinces (Yunnan, Guangxi, and Guangdong) in southern China. The MaxEnt model predicted that the suitable habitat for both species will increase with increased greenhouse emission scenarios. We also found that with the further increase in greenhouse emissions *M. thibetana* is expected to migrate to western China, and *M. arctoides* is expected to migrate to western or eastern China. This reinterpretation of the distribution of *M. thibetana* and *M. arctoides* in China, and predicted potential suitable habitat and possible migration direction, may provide new insights into the future conservation and management of these two species.

KEYWORDS

global climate change, habitat shift, *Macaca arctoides*, *Macaca thibetana*, MaxEnt model, population distribution

Abbreviations: AUC, a receiver operating characteristic curve; MaxEnt, maximum entropy; SDM, species distribution models; SSPs, shared social economic paths.

Wen-Bo Li and Pei-Pei Yang are contributed equally to this study.

1 | INTRODUCTION

Global climate change is one of the main threats to ecosystem health and biodiversity. It affects the spatiotemporal distribution, abundance, activity, and micro-environmental utilization of species (Brunsdon et al., 2007; Gavin et al., 2014; Luo et al., 2015; Pecl et al., 2017; Stewart et al., 2020; Zeng et al., 2021; J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021). A species geographical distribution depends on its environmental tolerance, dispersal limitation, and biological interaction with other species (Pecl et al., 2017; L. P. Sales et al., 2019; K. Zhang et al., 2018). As climate changes, species must migrate, adapt, or face extinction (Berg et al., 2010; L. Sales et al., 2020; Sun et al., 2020).

Scholars have extensively documented range shifts in the latitude and elevation of species distribution (Chen et al., 2011; Deb et al., 2020; J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021). For example, Chen et al. (2011) undertook a meta-analysis of available studies of latitudinal (Europe, North America, and Chile) and elevational (Europe, North America, Malaysia, and Marion Island) range shifts for species in a variety of taxonomic groups. The authors found that the ranges of many terrestrial organisms, such as trees, insects, and mammals have recently shifted to higher elevations and latitudes at median rates of 11.0 m per decade and 16.9 km per decade, respectively. Terrestrial species on mountainsides migrated upslope to escape warm lowlands (Chen et al., 2009). However, species-specific physiological, behavioral, ecological, and evolutionary responses and habitat fragmentation of animals can also cause species distribution to lag behind climate change if they cannot adapt quickly without increasing the risk of extinction (Pecl et al., 2017). These scenarios will ultimately alter the ecosystem balance and decrease biodiversity (Chen et al., 2011; T. L. Graham et al., 2016; Pecl et al., 2017). Thus, predicting the impact of climate change on species distribution is one of the hot spots in conservation biology and ecology, which could provide a reference for species conservation and long-term management strategies.

The International Union for Conservation of Nature (IUCN; 2021) classified *Macaca thibetana* as Near Threatened and endemic to east-central and south China (J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020). It is one of the most widespread primate species in China, which is distributed across 13 provinces (i.e., Zhejiang, Anhui, Fujian, Jiangxi, Hubei, Hunan, Guangdong, Guangxi, Sichuan, Guizhou, Yunnan, Gansu, and Tibet) and occupies subtropical evergreen broad-leaved forest zones between 600 and 2400 m above sea level (asl; J. H. Li, 1999; J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020; Q. Zhao et al., 1991). Its estimated population size is 20,000 individuals (B. Li et al., 2018). Alternatively, *Macaca arctoides* is classified by the IUCN as Vulnerable. This species is distributed in southern and southwestern China but limited to Guangdong, Guangxi, and Yunnan, occupying subtropical evergreen broad-leaved forest zones between 1500 and 3000 m asl. and in southern part of Guangxi, *M. arctoides* also lives in low altitude limestone hill. It's estimated population size is about 3700 (IUCN, 2021; B. Li

et al., 2018; Ruan & Huang, 2014). Both species may play an essential role in seed dispersal to maintain the stability of the temperate and subtropical forest ecosystems, according to previous studies on the seed dispersal of primates (Razafindratsima et al., 2018; Tsuji & Su, 2018). Specifically, macaques may act as dispersal agents of medium to large seeds, which may be particularly important in environments where other animals have been lost as a result of human activity. *M. thibetana* and *M. arctoides* are terrestrial and vulnerable to traps; thus, both their population sizes and distribution ranges have notably decreased (IUCN, 2021).

M. thibetana and *M. arctoides* are relatively similar in that they have a large body size and brownish dorsal pelage coloration. They only differ in the structure of the male and female reproductive organs, details of their pelage, facial skin coloration, and cranial morphology. These species have been frequently confused or regarded as only subspecifically distinct due to their superficial similarities and geographic proximity (Fooden et al., 1985; J. H. Li, 1999; J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020). As such, only experienced researchers can accurately distinguish the two species in the wild. However, the efforts of Chinese researchers are leading to the preliminary determination of the general distribution of these two species in China. While taxonomic disputes and evolutionary history have been resolved in recent genomic studies (Fan et al., 2014, 2018), less is known about their geographic distribution in China.

Conducting a comprehensive investigation of a widely distributed species on detailed spatial and temporal scales is extremely difficult, and data on species distribution sites are sporadic (Jiang et al., 2020). Moreover, researchers tried to shift from already well-documented impacts of climate change to predict species distribution respond to future climate (X. Zhao et al., 2019). Species distribution models (SDMs) simulate the suitability of species habitats at varying spatial scales based on available data and habitat characteristics (Chala et al., 2019; Watts et al., 2019; K. Zhang et al., 2018). They can also use predicted climate data to estimate the present and future distribution patterns of species (Deb et al., 2020; L. P. Sales et al., 2019; K. Zhang et al., 2018). Several SDMs, such as CLIMEX, Domain, genetic algorithm for rule-set production, and maximum entropy (MaxEnt), have been used to evaluate the ecological needs, responses, and distribution patterns of species (Byeon et al., 2018; Chala et al., 2019; Owens et al., 2011; Pattison & Mack, 2008; K. Zhang et al., 2018). Of these models, MaxEnt uses actual presence data of species and corresponding environmental variables to calculate the ideal state of species distribution under certain niche constraints, that is, the possible distribution of species in a predicted area when the entropy is maximum (Byeon et al., 2018). This model differs from other models in the requirement of data on species distribution sites, the setting of model parameters, and the treatment of environmental variables (Pattison & Mack, 2008; C. Wu et al., 2021; K. Zhang et al., 2018). The MaxEnt model has been widely used due to its small sample demand, short running time, simple operation, and high precision in predicting the distribution patterns of certain plant species under different scenarios of climate change (Pattison &

Mack, 2008; C. Wu et al., 2021; K. Zhang et al., 2018). Recently, this model has also been widely used in predicting range shifts of animals and their suitable habitat ranges at varied spatial scales. The accuracy of the obtained results is widely recognized even in the case of a limited number of samples (Chala et al., 2019; Luo et al., 2015; L. P. Sales et al., 2019; X. Zhao et al., 2019).

The current study used the MaxEnt model to predict the spatiotemporal distribution patterns of *M. thibetana* and *M. arctoides* in China. We aimed to determine (1) which environment and climatic variables influence their current distribution in China (2) the spatiotemporal shift in the distribution range of these species by simulating three realistic scenarios with current and future trends in climate change and (3) the spatiotemporal distribution of their suitable habitats based on future climatic conditions to deduce a practical conservation framework for conservation and management.

2 | METHOD

2.1 | Occurrence data collection

We obtained occurrence data of *M. thibetana* and *M. arctoides* in China from previous studies (1980–2021) and included our previous field transect surveys in several provinces, including Anhui, Guangdong, Guangxi, Yunnan, Sichuan, Hubei, and Gansu; We downloaded other occurrence data from the Global Biodiversity Information Facility (<https://www.gbif.org/>), and the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>). We referred to the longitudes and latitudes of recorded locations using Google Earth. Before analysis, we manually omitted sites with unknown records, errors,

and duplicates (within a grid cell of $10 \times 10 \text{ km}^2$). However, we identified a few locations beyond the known distributions of these two species according to previous infrared camera monitoring, interviews with specialists, and literature collection. Finally, we collected 192 and 80 records valid distribution points for *M. thibetana* and *M. arctoides*, respectively, to map their distribution patterns (Figure 1; Supporting Information Material Table 1).

2.2 | Predictive environmental variables

Land cover, habitat characteristics, and climate factors influence species distribution. The distribution of the two macaque species are significantly correlated with elevation and land cover. They select different elevations and slopes across the seasons, and both prefer subtropical mixed broadleaf evergreen-deciduous forest (Fooden et al., 1985; Wada et al., 1987; Q. Zhao & Deng, 1988). We classified land cover into cropland, forest, grassland, shrubland, wetland, water, tundra, impervious surface, bare land, snow/ice-disturbed according to global land cover data (download from <https://data.ess.tsinghua.edu.cn/>) in this study. The WorldClim data set provides bioclimatic data (Version 2.0, www.worldclim.org/) for the period 1970–2000 and future climate data (i.e., 2050s: 2041–2060; 2070s: 2061–2080) with a 2.5' spatial resolution. We used the predictions of the general circulation model under the shared social economic paths (SSPs) proposed by the Coupled Model Intercomparison Project Phase 6 of IPCC of the Intergovernmental Panel on Climate Change to predict future climate change (Popp et al., 2017). Moreover, we selected the Beijing Climate Center Climate System Model (BCC-CSM2-MR) as the climate system model, which was

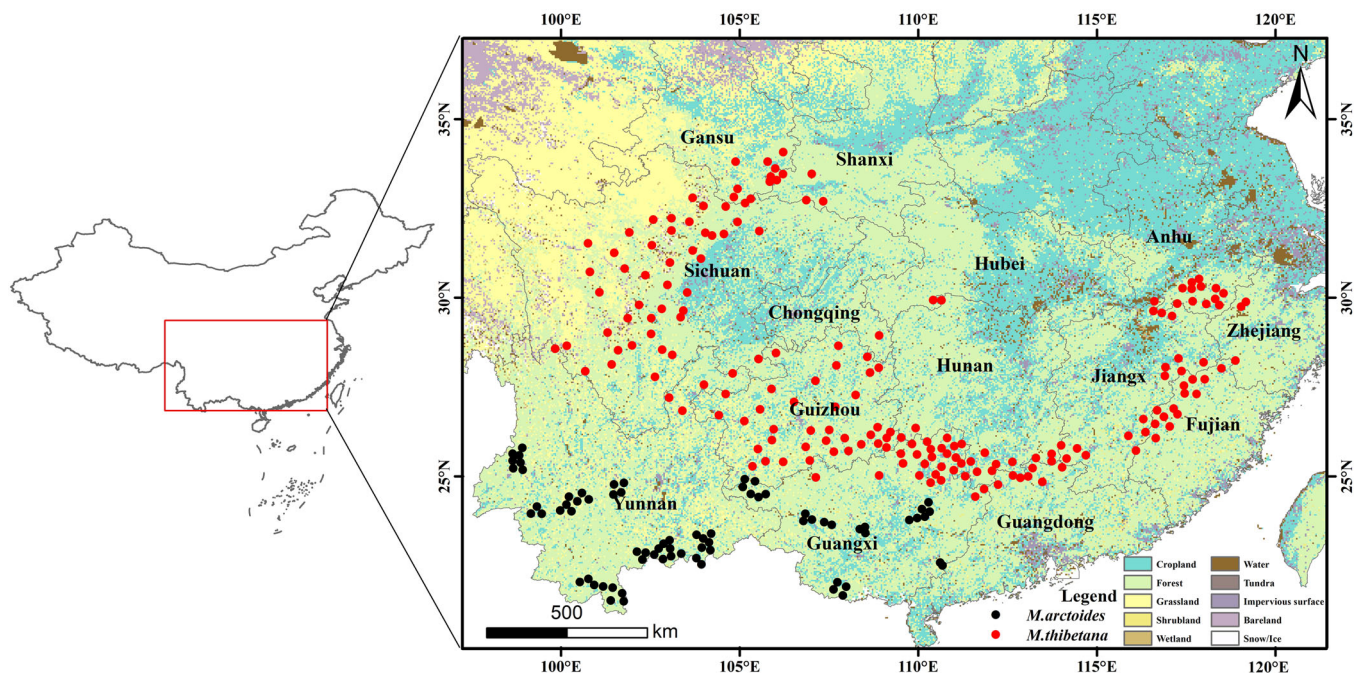


FIGURE 1 Occurrence data and distribution patterns of *Macaca thibetana* and *Macaca arctoides* in China.

TABLE 1 Information on elevation, climatic factors, and land cover included in the MaxEnt model, which influence the distribution of *Macaca thibetana* and *Macaca arctoides* in China.

Abbreviations	Description
Ele	Elevation (m)
Bio_1	Annual Mean Temperature (°C)
Bio_2	Mean Diurnal Range (mean of monthly [max temp-min temp]) (°C)
Bio_4	Temperature Seasonality (standard deviation * 100) (C of V)
Bio_7	Temperature Annual Range (Bio5–Bio6) (°C)
Bio_8	Mean temperature in Wettest Quarter (°C)
Bio_10	Mean temperature in Warmest Quarter (°C)
Bio_12	Annual Precipitation (mm)
Bio_14	Precipitation in Driest Month (mm)
Bio_15	Precipitation Seasonality (C of V)
Bio_16	Precipitation in Wettest Quarter (mm)
Bio_18	Precipitation in Warmest Quarter (mm)
Lac	Land Cover Types (Cropland, Forest, Grassland, Shrubland, Wetland, Water, Tundra, Impervious Surface, Bare Land, Snow/Ice-Disturbed)

developed at the National Climate Center, because it demonstrates the best performance in East Asia (T. Wu et al., 2019). Scholars in China typically used BCC-CSM2-MR to predict species distribution (J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021). SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 represent a low, medium, medium-to-high, and high-forcing scenarios, respectively (Fischer et al., 2005). We selected SSP1-2.6, SSP2-4.5, and SSP5-8.5 as representative of the minimum, moderate, and maximum greenhouse emission scenarios, respectively, to predict the potential future spatial distribution of *M. thibetana* and *M. arctoides*. To overcome the over-fitting problem in the model results caused by the multi-collinearity of 19 climatic factors, we screened variables using Spearman's correlation coefficient >0.8 and omitted highly correlated climatic factors (M. H. Graham, 2003). Finally, we identified 11 climatic factors (Table 1).

2.3 | Present and future habitat distribution predictions

We used MaxEnt 3.4.1 to predict the current and future distribution of the *M. thibetana* and *M. arctoides* in China (<https://www.cs.princeton.edu/wschapire/Maxent/>). We supplied their occurrence data and 13 environmental variables (Table 1) to MaxEnt. We randomly selected 75% for each species and 25% as the training and test set, respectively. The algorithm performed 1000 iterations of these processes or continued until convergence (threshold:

0.00001; Phillips & Dudík, 2008). We transformed the output into raster format using ArcMap 10.4 ArcGIS for further analysis. Moreover, we used the values of the area under a receiver operating characteristic curve (AUC) to calibrate and validate the robustness of the evaluation using the MaxEnt model (K. Zhang et al., 2018). The values ranged from 0.5 to 1, with high values implying high levels of the prediction accuracy of the model (reference value: >0.9). MaxEnt used the Jackknife method to calculate the contribution rate of environmental factors to species distribution and determine the primary influential climatic factors. The range of potential species distribution was 0-1, which was classified into the following four categories, namely, “highly suitable” (0.6–1), “moderately suitable” (0.4–0.6), “poorly suitable” (0.2–0.4), and “unsuitable” (<0.2) (K. Zhang et al., 2018). We divided the area of the predicted habitats into three categories: “range expansion,” “range contraction,” and “no change.” Subsequently, we estimated the spatial range of the three types of areas.

2.4 | Distribution change and migration paths

The study used ArcGIS to determine the central point of the suitable habitat of *M. thibetana* and *M. arctoides* under the present and future climatic conditions. The procedure is as follows (Mu et al., 2022): first, we extracted the most suitable habitat areas under different climatic conditions across species using ArcGIS software; second, we generated the central point of each habitat area using the SDM toolbox. Finally, we examined the central point migration under different scenarios of climate change (Brown et al., 2017; Mu et al., 2022).

3 | RESULTS

3.1 | Optimal model and accuracy

Given the datasets for training (75%), testing (25%), and random prediction, the accuracy of the models for *M. thibetana* and *M. arctoides* was better than those of random prediction models. The AUC training value was >0.9 (*M. thibetana*: the training data = 0.953, test data = 0.935; *M. arctoides*: training data = 0.984, test data = 0.977). The simulation results indicated that the MaxEnt model output provided satisfactory results. Currently, the model predicted that the highly suitable areas for *M. thibetana* are concentrated in the eastern (Anhui, Zhejiang, Fujian, and Jiangxi), central (Hubei and Hunan), southern (Guangdong and Guangxi), and southwestern (Chongqing, Sichuan, and Guizhou) China (Figure 2a1). The moderately suitable areas of *M. thibetana* were similar to the highly suitable areas (Figure 2a1).

Currently, the model predicts that the highly suitable areas for *M. arctoides* are concentrated to southeast Yunnan (Figure 2b1). The moderately suitable areas cover the majority Yunnan, western, and eastern Guangxi (Figure 2b1).

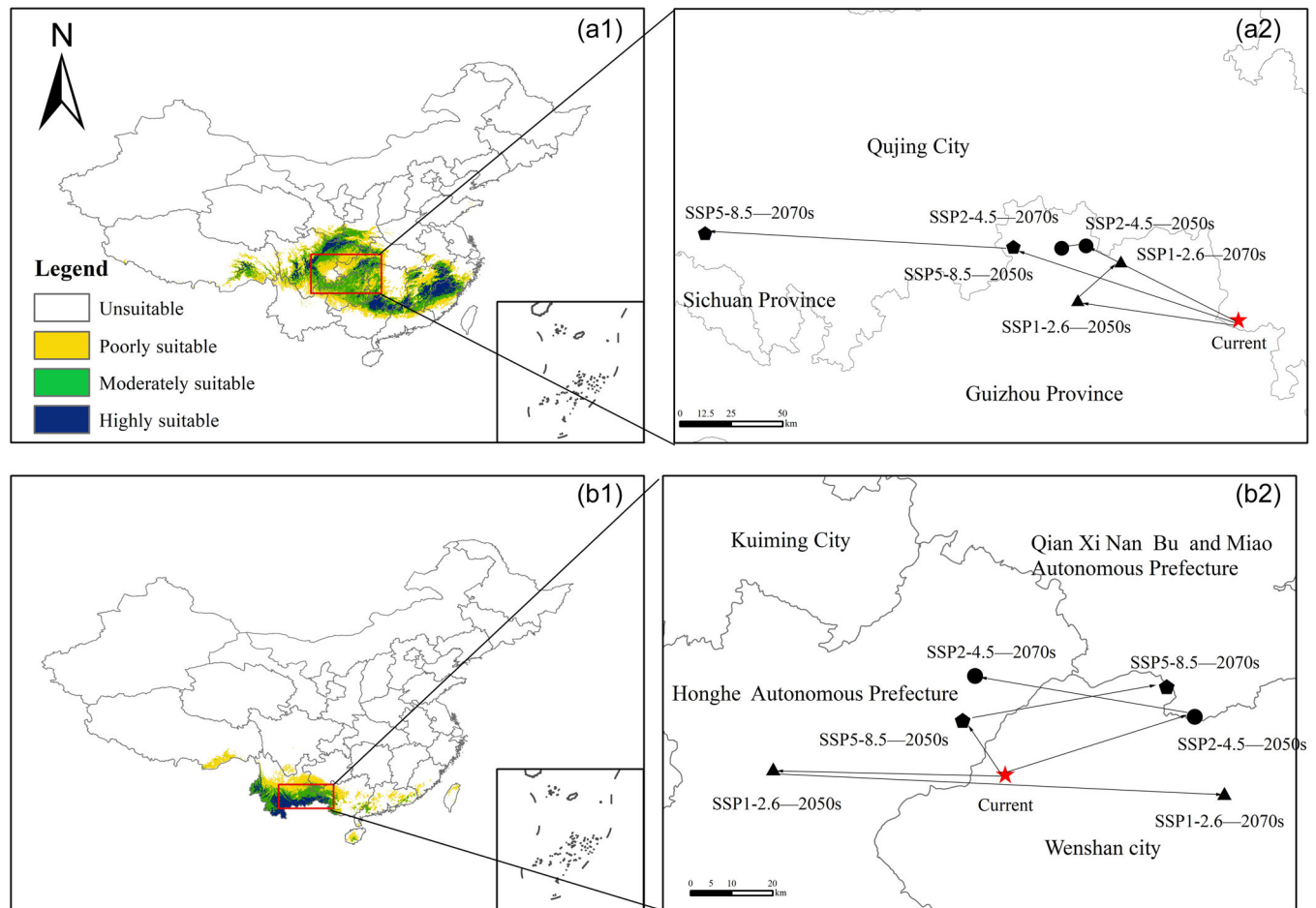


FIGURE 2 Potential distribution patterns (a1 and b1) and migration paths (a2 and b2) of *Macaca thibetana* and *Macaca arctoides* under the present and future scenarios of climate change in China: A1 and A2 for *M. thibetana*; B1 and B2 *M. arctoides*. The arrows indicate the trend of predicted changes in suitable habitats over time. SSPs: shared socioeconomic paths.

3.2 | Climate factors influencing the spatiotemporal distribution of the macaque species

Annual precipitation (Bio12, 34.01%), annual temperature range (Bio7, 22.80%), and land cover (22.22%) exerted maximum influence on the distribution of *M. thibetana* (Table 2). Whereas temperature seasonality (Bio4, 52.31%) and precipitation in the driest month (Bio14, 18.48%) exhibited the maximum influence on the distribution of *M. arctoides*.

Notably, the study used environmental factors with a contribution rate of more than 10% to conduct an independent analysis of the impact of potential habitats. For *M. thibetana*, a higher or lower temperature annual range (with an annual temperature range from 26°C to 29°C (bio7)) will reduce their suitability when the probability of presence is less than 0.5 (Figure 3a). Likewise, suitable habitat will decrease with an annual precipitation between 1281 mm and 2251 mm (bio12; Figure 3b). The main land cover type that will affect *M. thibetana* is forest when suitability reaches a higher level, approximately 0.61.

TABLE 2 Proportional contributions of the environmental predictors on the possible spatial distribution of *Macaca thibetana* and *Macaca arctoides*.

Variables	Contribution (%)	
	<i>Macaca thibetana</i>	<i>Macaca arctoides</i>
Bio_4	8.53	52.31
Bio_7	22.80	3.32
Bio_12	34.01	0.68
Bio_14	-	18.48
Land cover	22.22	1.23

Note: To conduct an independent analysis on the impact of the potential habitats of *M. thibetana* and *M. arctoides*, we used variables with a contribution of more than 10%.

For *M. arctoides*, higher or lower temperature seasonality will reduce suitability (i.e., less than 0.5) (Figure 3c) with the response curves for temperature seasonality at between 1°C and 4°C (bio4) and the precipitation of the driest month more than 0 mm (bio14; Figure 3d).

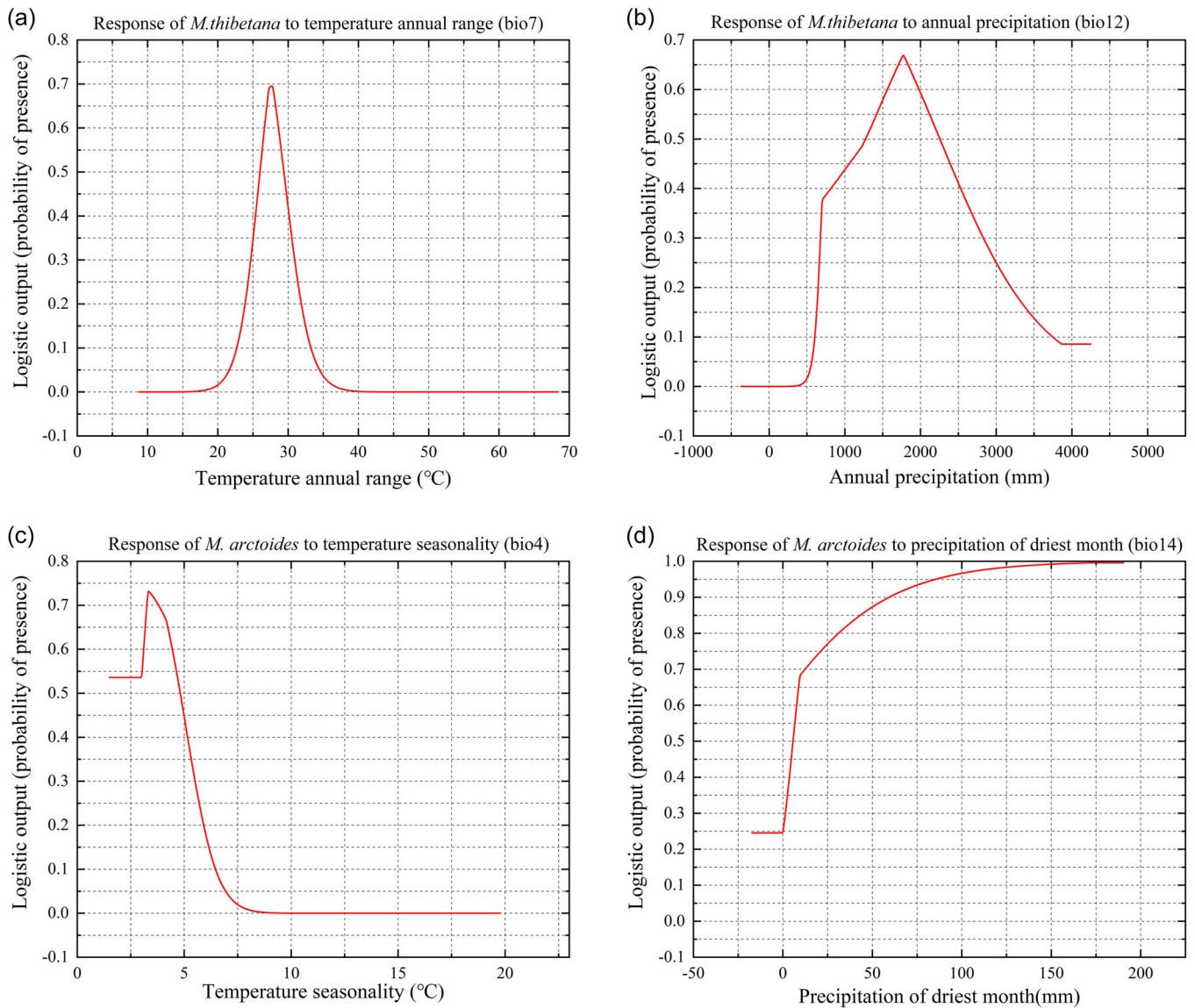


FIGURE 3 Response curves of primary climatic and land cover factors are included in the MaxEnt output for *Macaca thibetana* (a, b) and *Macaca arctoides* (c, d). The variables with a contribution rate of more than 10% were used to conduct independent analysis on the impact of potential habitats. (a) Response of *M. thibetana* to annual temperature range shift (bio7, contribution rate: 22.80%); (b) Response of *M. thibetana* to annual precipitation (bio12, contribution rate: 34.01%); (c) Response of *M. arctoides* to temperature seasonality (bio4, contribution rate: 52.31%); (d) Response of *M. arctoides* to precipitation of driest month (bio14, contribution rate: 18.48%).

3.3 | Changing suitable habitat areas under future climate change scenarios

By comparing suitable area changes across six future scenarios in climate change, we found that the total suitable habitat for *M. thibetana* will represent 13.33%, 14.38%, and 14.32% of the total land area in China by the 2050s for SSP1-2.6, SSP2-4.5, and SSP5-8.5, which will be decreased by 0.37%, increased by 0.68%, and 0.62%, respectively. Thus, using the three models, suitable habitat will be increased except for SSP1-2.6 (Figure 4).

The suitable habitat for *M. thibetana* will represent 13.84%, 15.03%, and 14.32% of the whole land area of China for SSP1-2.6, SSP2-4.5, and SSP5-8.5, which will increase by 0.14%,

1.33%, and 0.62%, respectively, compared with current climate conditions. Generally speaking, the potential spatial distribution of *M. thibetana* under different climate scenarios will exhibit an increasing trend in the 2070s (Figure 4).

By the 2050s, for SSP1-2.6, SSP2-4.5, and SSP5-8.5, the total suitable habitat for *M. arctoides* will represent 4.44%, 5.33%, and 5.02% of the total land area of China, which will decrease by 0.12%, increase by 0.77%, and 0.46%, respectively, compared with current climate conditions. For SSP2-4.5 and SSP5-8.5, the total suitable habitat for *M. arctoides* will represent 5.33% and 5.02% of the total land area in China, which will increase by 0.77% and 0.46%, respectively, compared with modern climate conditions. Simply put, the potential distribution of *M. arctoides* under different scenarios of

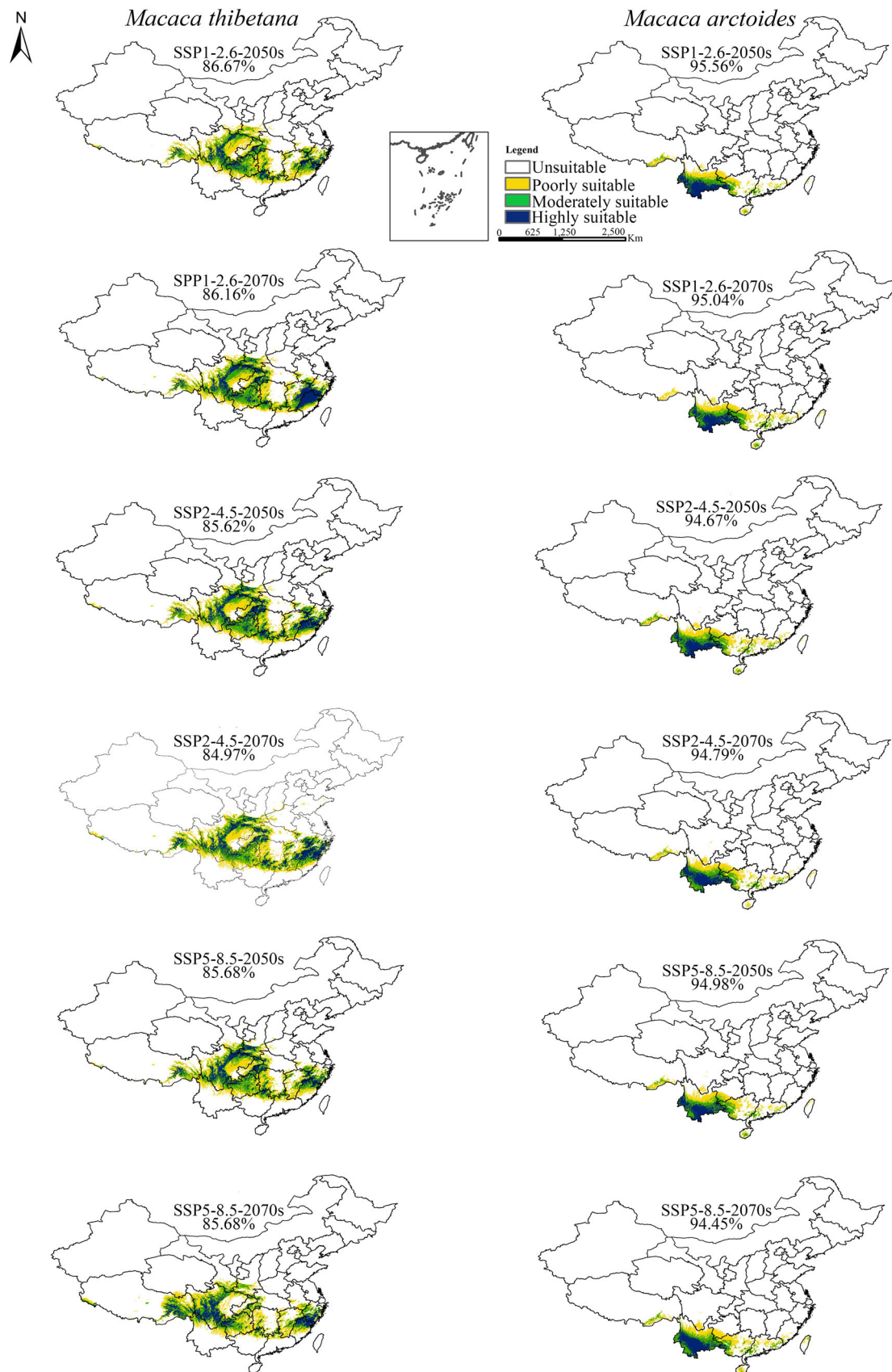


FIGURE 4 Future potential geographical distributions of *Macaca thibetana* and *Macaca arctoides* in China from the 2050 to 2070s according to climate scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5. Percentage refers to the proportion of unsuitable habitat area in the total land area in China, excluding the area of territorial waters in the statistics.

climate change in the 2050 s exhibits an increasing trend except for SSP1-2.6 (Figure 4).

By the 2070 s, for SSP1-2.6, SSP2-4.5, and SSP5-8.5, the total suitable habitat for *M. arctoides* will represent 4.96%, 5.21%, and 5.55% of the whole land area in China, which will increase by 0.4%, 0.65%, and 0.99% compared with current climate conditions. The potential spatial distribution of *M. arctoides* under different climate scenarios in the 2070 s displays an increasing trend (Figure 4).

Under the six future climate scenarios, the range expansion *M. thibetana* from $1.14 \times 10^5 \text{ km}^2$ to $3.6 \times 10^5 \text{ km}^2$ in south Anhui, and Guizhou, north Zhejiang, and Jiangxi, west Guangxi, east Yunnan, Sichuan, and Tibet (Figure 5c; Table 3). The range contraction from $1.20 \times 10^5 \text{ km}^2$ to $3.00 \times 10^5 \text{ km}^2$ and was predicted for central and eastern Hubei, northeast Jiangxi, southeast Zhejiang, central Fujian, Guangxi, Guangdong, and southern Gansu. (Figure 5c and Table 3).

Alternatively, the range expansion of *M. arctoides* from $0.21 \times 10^5 \text{ km}^2$ to $1.13 \times 10^5 \text{ km}^2$ in southeast Tibet, northern Yunnan, southern Sichuan, and central Guizhou (Figure 5d; Table 3). The range contraction from $0.06 \times 10^5 \text{ km}^2$ to $0.33 \times 10^5 \text{ km}^2$ and was predicted for western Guangdong, central Guangxi, southwestern Yunnan, and southern Guizhou (Figure 5d and Table 3).

3.4 | Change in centroid and migration paths

We used barycenter migration analysis to characterize the changes in the distribution pattern under the six climate change scenarios due to the irregular shape of the suitable habitat areas for the *M. thibetana* and *M. arctoides*. We found that the barycenter of the suitable habitat areas for *M. thibetana* under the present climate change scenario is located in YouYang Tujia & Miao in Northeast Guizhou ($108^\circ 25' 41.3184''$, $28^\circ 40' 48.0576''$). In contrast, the species is predicted to migrate to the west under different climate scenarios in the 2050 s and 2070 s. Among them, SSP5-8.5(2070 s) predicted the farthest migration ($106^\circ 5' 23.3592''$, $29^\circ 3' 37.1808''$), and SSP2-4.5 (2050 s) predicted the second farthest migration ($107^\circ 44' 38.3316''$, $29^\circ 0' 13.716''$). However, under the SSP1-2.6 scenario, *M. thibetana* was predicted to first migrate to the west in the 2050 s then to the east in the 2070 s ($107^\circ 54' 46.7892''$, $28^\circ 56' 11.1192''$) (Figure 2a2).

Under the present climate change scenario, the barycenter of the suitable habitat areas for *M. arctoides* was located in northeast Wenshan city, in southeast Yunnan ($103^\circ 51' 34.2792''$, $24^\circ 13' 57.9288''$). Under different climate change scenarios in the 2050 s and 2070 s, the barycenter of the suitable habitat areas was predicted to migrate to the west or east (Figure 2b2). Among them, SSP1-2.6 (2050 and 2070 s) exhibited the farthest migration distance, first migrating to the west in the 2050 s and then to the east in the 2070 s (Figure 2b2). SSP2-4.5 exhibited the second farthest estimate, first migrate to the east in the 2050 s and then to the west in the 2070 s (Figure 2b2). Under the SSP5-8.5 scenario, exhibited the slowest prediction, first to migrate to the west in the 2050 s and then to the east in the 2070 s (Figure 2b2).

4 | DISCUSSION

This study obtained the current occurrence data for *M. thibetana* and *M. arctoides* in China and added environment and climate variables using the MaxEnt model. We found that temperature range (bio7), annual precipitation (bio12), and land cover (forest) are the main factors affecting the distribution of *M. thibetana*, and temperature seasonality (bio4) and precipitation in the driest month (bio14) for *M. arctoides*. Currently, *M. thibetana* is mainly concentrated in central, eastern, southern, and southwestern China, and *M. arctoides* is mainly distributed in certain provinces (Guangxi, Guangdong, and Yunnan) in southern China. The MaxEnt model predicted that in the future, the suitable habitat for both species will continue to expand with the increase in greenhouse emission scenarios. We also found that with the further increase in greenhouse emissions, *M. thibetana* is expected to migrate to western China and *M. arctoides* to western or eastern China.

In the current and future scenarios, the distribution of *M. thibetana* is consistent with the findings of the previous studies (Li, 1999; J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020). The current results demonstrate that global warming would increase the suitable habitat of *M. thibetana*. These findings are in agreement with those previous studies, which suggest that *M. thibetana* prefers to live in middle-high mountains, similar to *Rhinopithecus bieti* (Li, 1999; Luo et al., 2015; Q. Zhao & Deng, 1988). The major impact of climate change is expected to be an increase in temperature. For species distributed at medium to high altitudes, high-altitude areas will also become suitable habitats (Chen et al., 2011; X. Zhao et al., 2019).

The suitable habitat for *M. arctoides* is restricted to southwestern China. It is limited to remote mountainous areas, such as Yunnan, Guangxi, Guizhou, Guangdong, and Fujian, where suitable habitat is increasing with an expected increase in global temperature. Large-scale hydrothermal conditions (incorporating temperature and precipitation) are essential for determining species distribution. Limiting factors include deforestation, hunting, group size, sex ratio, competition, food habits, and resource availability which are directly related to species distribution (Jiang et al., 2020; Kurihara & Hanya, 2015, 2018). In recent years, many previously destroyed forests have been restored, and the decline in hunting has had a positive effect on the populations of many endangered species and increased their distribution (Luo et al., 2015; Ruan & Huang, 2014; X. Zhao et al., 2019). These may also be the main reasons for the increase in the distribution of *M. arctoides*.

Our model predicted that temperature range (bio7), annual precipitation (bio12), and land cover (forest) are the critical factors that influence the distribution of *M. thibetana*. Annual temperature and precipitation directly affect the food availability of primates and may eventually change their spatial distribution (Cui et al., 2019; Khatiwada et al., 2020; Kurihara & Hanya, 2015; Q. Zhao et al., 1991). *M. thibetana* feeds on different kinds of foods across seasons and changes its home range size seasonally with shifting food availability (Xiong & Wang, 1988; Q. Zhao & Deng, 1988; Q. Zhao et al., 1991).

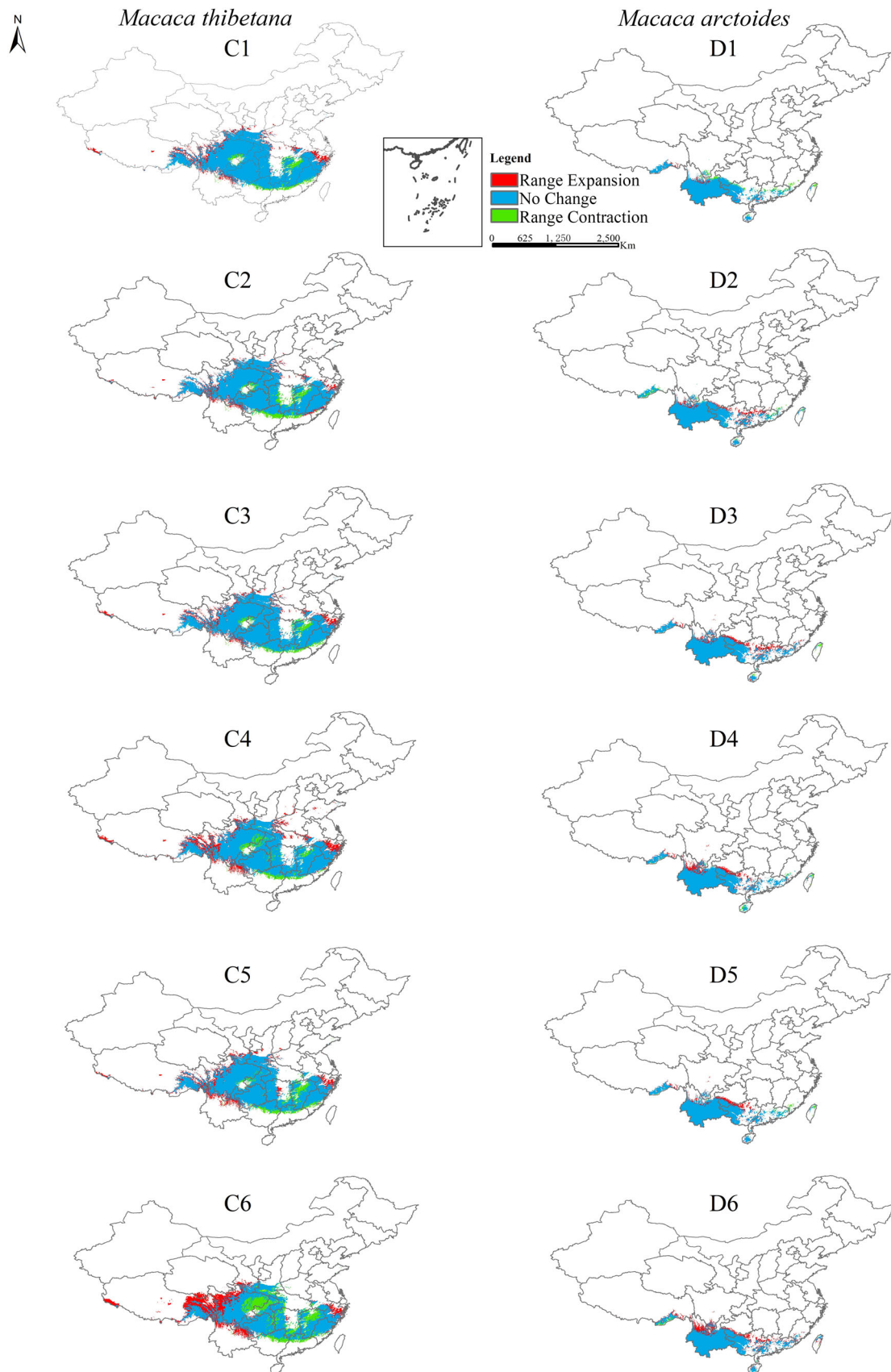


FIGURE 5 Future potential distributions of *Macaca thibetana* (C) and *Macaca arctoides* (D) in China from the 2050 to 2070 s according to the climate scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5.

TABLE 3 Range expansion, contraction, and no-change distribution areas for *Macaca thibetana* and *Macaca arctoides* under the six future climate scenarios in China.

Climate scenarios	Species					
	<i>M. thibetana</i>			<i>M. arctoides</i>		
	Area ($\times 10^5$ km ²)					
	Range expansion	Range contraction	No-change	Range expansion	Range contraction	No- change
SSP1-2.6-2050s	1.14	1.52	12.75	0.21	0.33	4.58
SSP1-2.6-2070s	1.34	1.23	13.05	0.63	0.19	4.73
SSP2-4.5-2050s	1.63	0.96	13.32	0.88	0.06	4.86
SSP2-4.5-2070s	2.54	1.2	13.07	0.81	0.11	4.8
SSP5-8.5-2050s	1.9	1.28	12.99	0.61	0.12	4.8
SSP5-8.5-2070s	3.6	3	11.28	1.13	0.08	4.84

Abbreviation: SSPs, shared social-economic paths

When the temperature rises, *M. thibetana* has highly flexible adaptability, for example, under low or high-temperature conditions, they exhibit shorter daily range distances (Xiong & Wang, 1988) and in the cold winter, they can warm each other by huddling (Ogawa, 2003).

Conversely, temperature seasonality (bio4) and precipitation in the driest month (bio14) are the main factors that influence the distribution of *M. arctoides*. These results illustrate that *M. arctoides* has seasonal constraints. Given its pattern of breeding seasonality, the temperature may act as a reproductive regulator for the onset of estrus and mating in *M. arctoides* (Smith, 1984). They mostly live in southwest China, which has pronounced dry and rainy seasons and has been characterized by seasonally variable rainfall. These variables influence the yield of young leaves and fruits and subject resident primates to marked fluctuations in food availability (J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020). A previous study showed that during the dry season, primates living in these regions are expected to face severe food shortages (J. Li, Fan, et al., 2020; B. Li, He, et al., 2020; Y. Li, Ma, et al., 2020; J. S. Li, Sun, et al., 2020).

With climate change, the original habitats may no longer meet the needs of these macaque species, and they are expected to migrate to new habitats (K. Zhang et al., 2018; J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021). This study predicted that the *M. thibetana* and *M. arctoides* would migrate toward the western or eastern of China, and the migration distance would increase with the increase in temperature. These predictions are similar to those for other animals, such as antelopes (J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021) and the Sichuan snub-nosed monkeys (Luo et al., 2015; X. Zhao et al., 2019). Animal migration to higher latitudes may enable them to adapt to high temperatures and land-use changes (Estrada et al., 2017; X. Zhao et al., 2019), but inter-specific competition may also influence species migration (Khatiwada et al., 2020; L. Sales et al., 2020). However, species diversity is expected to decrease with the increase in global temperature (Pecl et al., 2017). With the increase in temperature, vegetation diversity in the original habitat is expected to decrease. In turn, niche overlap

among other animals in the same region could increase inter-specific competition and influence migration patterns (J. Zhang, Jiang et al., 2021; S. Zhang, Liu, et al., 2021). Despite the well-known behavioral flexibility of primates to adapt to novel environmental conditions, they have relatively limited dispersal abilities for their body size, slow reproduction, low population densities, dietary requirements, and thermoregulation, and many of them might already have surpassed their thermal tolerance to climate conditions (Estrada et al., 2017). Thus, we can expect that both species, will be widely exposed to extreme changes in climatic conditions, likely being highly vulnerable to and facing an elevated risk of extinction due to climate change.

5 | CONCLUSION

The results of the present study were consistent with the climatic factors and spatial distribution of *M. thibetana* and *M. arctoides* determined in previous research, suggesting that the area of suitable habitat predicted by the MaxEnt model was consistent with measurements. This study simulated the effects of climate change scenarios on the spatiotemporal distribution of *M. thibetana* and *M. arctoides*. We demonstrated that both species will likely be susceptible to climate change. However, they exhibited different spatiotemporal distribution patterns across climate change scenarios. The suitable habitat for *M. thibetana* and *M. arctoides* is likely to increase, but the two species are expected to exhibit different migration patterns. The results provide valuable references for formulating the adaptive ability of *M. thibetana* and *M. arctoides* to deal with climate change and may provide new insights into the future conservation and management of these two species.

AUTHOR CONTRIBUTIONS

Wen-Bo Li: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); software (supporting); validation (lead); visualization (lead); writing-original draft (lead); writing-review and editing (lead). **Pei-Pei Yang:**

Conceptualization (supporting); investigation (equal); data curation (equal); formal analysis (lead); software (lead); validation (equal); writing-original draft (equal); writing-review and editing (equal). **Dong-Po Xia:** Conceptualization (equal); data curation (supporting); investigation (equal); methodology (equal); writing-review and editing (supporting); **Ming Li and Jin-Hua Li:** Funding acquisition (lead); investigation (supporting); project administration (lead); resources (lead); writing-review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

All research protocols reported in this manuscript were approved by the Chinese Wildlife Management Authority. The study was completely observational in nature and did not involve invasive experimentation on wild primates. Thus, no review from an institutional ethics committee in China was required. This research followed the Wildlife Protection Law of the People's Republic of China. All research reported here adhered to the regulatory requirements of Huangshan Garden Forest Bureau, China, where the study took place.

ORCID

Wen-Bo Li  <http://orcid.org/0000-0003-4867-0479>

Dong-Po Xia  <http://orcid.org/0000-0002-1266-2285>

Ming Li  <http://orcid.org/0000-0001-5689-6270>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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