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RESEARCH ARTICLE

Human activity and climate change accelerate the extinction risk to non-human primates in China

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Abstract

Human activity and climate change affect biodiversity and cause species range shifts, contractions, and expansions. Globally, human activities and climate change have emerged as persistent threats to biodiversity, leading to approximately 68% of the ~522 primate species being threatened with extinction. Here, we used habitat suitability models and integrated data on human population density, gross domestic product (GDP), road construction, the normalized difference vegetation index (NDVI), the location of protected areas (PAs), and climate change to predict potential changes in the distributional range and richness of 26 China's primate species. Our results indicate that both PAs and NDVI have a positive impact on primate distributions. With increasing anthropogenic pressure, species' ranges were restricted to areas of high vegetation cover and in PAs surrounded by buffer zones of 2.7–4.5 km and a core area of PAs at least 0.1–0.5 km from the closest edge of the PA. Areas with a GDP below the Chinese national average of 100,000 yuan were found to be ecologically vulnerable, and this had a negative impact on primate distributions. Changes in temperature and precipitation were also significant contributors to a reduction in the range of primate species. Under the expected influence of climate change over the next 30–50 years, we found that highly suitable habitat for primates will continue to decrease and species will be restricted to smaller and more peripheral parts of their current range. Areas of high primate diversity are expected to lose from 3 to 7 species. We recommend that immediate action be taken, including expanding China's National Park Program, the Ecological Conservation Redline Program, and the Natural Forest Protection Program, along with a stronger national policy promoting alternative/

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sustainable livelihoods for people in the local communities adjacent to primate ranges, to offset the detrimental effects of anthropogenic activities and climate change on primate survivorship.

KEYWORDS
climate change, extinction, human activity, primates, species distribution model, species richness

1 | INTRODUCTION

Human activities that convert natural environments into highly impacted and fragmented landscapes, along with climate change, represent significant threats to biodiversity in the 21st century (Duffy et al., 2022; Gorczynski et al., 2022; Kaisin et al., 2021; Parmesan, 2006). This is expected to result in the loss of one million animal and plant species (Barnosky et al., 2011; Ceballos et al., 2020; Dawson et al., 2011; Dobson et al., 2021; Song et al., 2021). Traditional biodiversity conservation measures aim to prevent species' population decline and local extinction by expanding areas of natural habitat, creating corridors to improve opportunities for migration and increased genetic diversity, limiting wildlife hunting and trapping, and establishing areas—geographic regions legally designated for the protection of biodiversity and cultural resources (Butchart et al., 2010; Pimm et al., 2014; Pringle, 2017). However, the challenges associated with protecting and maintaining biodiversity are dynamic, and success must be constantly re-evaluated to ensure that both short-term and long-term changes in the distribution, population size, demography, genetic variability, and availability of suitable habitat do not decrease in response to current and future human activities and climate change (Sgro et al., 2011).

The world's expanding human population is expected to reach 11.2 billion by the end of the century. This, along with the unsustainable demands for natural resources by a small number of consumer nations (Estrada et al., 2018), widespread deforestation, habitat conversion, biodiversity loss, urbanization, erosion of ecosystem services, and accelerating climate change, has created an impending mass extinction crisis (IPBES, 2019). At present, some 25% of the world's animal and plant species are threatened with extinction, including many of the world's non-human primates (primates from here on), our closest living biological relatives (IPBES, 2019). Primates (prosimians, tarsiers, monkeys, and apes) are the third most speciose mammalian radiation (522 extant species; only Rodentia and Chiroptera have more species), are an essential component of forest biodiversity, and contribute to forest regeneration as seed dispersers and pollinators (Estrada et al., 2022). Primates also play an important role in the livelihoods, cultures, and belief systems of many societies worldwide (Estrada et al., 2022; IUCN, 2022). Estrada et al. (2022) found that approximately 68% of primate species are threatened with extinction, principally because of global pressures to convert their habitats for agricultural production, extraction of natural resources, cattle ranching, disease transmission from contact with humans and domesticated animals, urbanization, and the construction of dams, roads, and rail networks. These human activities have resulted in significant habitat loss, primate population decline, and population fragmentation (Estrada et al., 2017; Galán-Acedo et al., 2021; Li, Chen, et al., 2022; Zhao, Garber, et al., 2021). In addition, human-mediated climate change, associated with warmer and drier conditions and more extreme climatic events (hurricanes, floods, cyclones, extended dry periods), represents a major driver exacerbating threats to primate survival (Bernard & Marshall, 2020; Carvalho et al., 2019; Graham et al., 2016; Zhang et al., 2019).

Field investigations and model simulations have demonstrated that primate species and their habitats are highly sensitive to climate change, especially to extended periods of increased temperatures (Condro et al., 2021; Graham et al., 2016; Stewart et al., 2020). And, although many primate species may be able to tolerate a temperature increase of 1.5–2.0°C (Graham et al., 2016), under a worst-case climate scenario, 74% of Neotropical primate species are likely to experience maximum temperature increases up to 7°C (Carvalho et al., 2019). Moreover, 86% of primate ranges in the Neotropics are expected to experience an increase in maximum temperature of >3°C (Carvalho et al., 2019). Given the resulting major reduction in the availability of suitable habitats, this will result in population extirpation (Carvalho et al., 2019; Parks et al., 2023; Zhang et al., 2019). For example, under a worst-case climate scenario, approximately one-quarter of Asian and African primates will face up to 50% range reduce by the year 2050 (Carvalho et al., 2019). And, although some species may be able to cope with these changes by dispersing into recently created suitable habitat or possibly adapting in situ, opportunities for dispersal or range shifts are expected to be extremely limited as habitats become more fragmented (Carvalho et al., 2019).

In addition, range shifts caused by climate change will likely result in a decrease in the proportion of primate ranges located outside of protected areas (PAs), which will bring new challenges to primate conservation (Li, Chen, et al., 2022; Zhang, Turvey, et al., 2021). The establishment of PAs with large buffer zones is an effective tool to protect against biodiversity decline (Hannah et al., 2007). Over time, however, climate change may result in the loss of suitable habitat within PAs, reducing a species' viability both inside PAs as well as in nearby buffer zones (Condro et al., 2021; Parks et al., 2023).

In the present study, we examine primate extinction risk in China. China is the second-largest economy in the world, has a population of 1.4 billion people, and ranks 82nd worldwide in its Human Development Index (IMF World Economic Outlook, 2022;

https://www.imf.org/). And, although in recent years the Chinese government has made positive efforts to protect biodiversity, in the process of China's transformation from an agricultural economy to a highly industrial economy, it has dramatically altered its natural landscape. For example, from 1950 to 2004, natural forests in China declined to only 30% of the total forest area (Li, 2004). In 2021, the total length of highways in China reached 5.28 million kilometers. China now ranks first worldwide in the length of its expressways and high-speed railway system (Maierdiyali et al., 2022). Industrial development, agriculture, urbanization, and infrastructure development have imperiled biodiversity and brought substantial environmental and conservation challenges nation-wide (Zhang et al., 2022). At the 15th meeting of the Conference of the Parties (COP15) in 2021 (phase one), the Chinese government proposed the Kunming Biodiversity Fund and the Kunming Declaration by contributing 1.5 billion yuan (~220 million U.S. dollars) for conservation. In phase two, the government negotiated the "Global Biodiversity Framework after 2020" (UN Environment Program: https://www.unep.org/), which is specifically designed to halt and reverse natural forest loss. Given its human capital of highly trained scientists and its rapidly expanding economy, China has the opportunity to promote highly effective conservation policies that have the potential to sustain, conserve, and effectively manage wildlife (Li et al., 2018).

China is the second-most primate-diverse country in Asia, with 28 species (two of which, the white-handed gibbon (*Hylobates lar*) and the northern white-cheeked gibbon (*Nomascus leucge*nys), have recently been extirpated in China). This diverse radiation includes three families and eight genera of lorises, macaques, langurs, snub-nosed monkeys, and gibbons. Some 80% of Chinese primate species are listed as threatened, and 92% are characterized by a declining population (IUCN, 2022; Li et al., 2022). The population sizes of 15–18 of these species contain less than 3000 wild individuals, making them highly susceptible to extinction (Li et al., 2018, 2022; Zhang et al., 2020). Most primate species in China have a highly circumscribed distribution, with only 1–2 species per province. The most primate biodiverse provinces are in western and southwestern China (Yunnan, Guangxi, Xizang, and Guizhou). Yunnan Province alone contains 15 primate species (Li et al., 2018).

All primate species in China currently inhabit fragmented landscapes and are distributed in small, isolated subpopulations with limited opportunities to exchange individuals or genetic information (Li et al., 2018, 2022; Zhao et al., 2019). Moreover, the majority of primate species in China (56%; 14/25) are distributed in areas with impoverished human populations (Zhao, Garber, et al., 2021; Zhao, Li, et al., 2021). In 2017, the Chinese Ministry of Environmental Protection defined poverty as living on less than 1 US$ a day. In addition, more than 80% of the poverty-stricken counties and 95% of the poverty-stricken people are in areas that are considered ecologically fragile and susceptible to expanding industrial agriculture and climate change (Zhao, Li, et al., 2021). As of 2021, China has lifted 832 counties and 98.99 million people out of poverty (Zhao, Li, et al., 2021). Increased income in local human communities has resulted in increased conservation efforts and protection for some primate species such as golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Yu et al., 2022), western black crested gibbons (*Nomascus concolor*) (Fan et al., 2022), François' langurs (*Trachypithecus francoisi*), white-headed langurs (*T. leucocephalus*) (Zhou & Huang, 2021), and rhesus macaques (*Macaca mulatta*) (Lu et al., 2018). However, for many other taxa (i.e., the newly described white-cheeked macaque, *M. leucogenys*) (Li et al., 2015); stump-tailed macaques, *M. arctoides* (Li et al., 2023); and central Himalayan langurs (*Semnopithecus schistaceus*) (Li et al., 2022), this has not been the case.

PAs represent an important conservation tool for primate survival. Currently, China has more than 11,800 PAs, covering 18% of its land area and 4.1% of its sea area (Feng et al., 2022). Over the past 20 years, the Chinese government has invested some 40 million yuan in combating environmental degradation and biodiversity loss through the creation of the Natural Forest Protection Program and expanding the system of local and national parks. However, national park creation has coincided with an expanding national and international tourism industry, and this has resulted in considerable environmental degradation and extensive infrastructure development in rural communities where these parks are located (Qiao et al., 2021). Moreover, despite the Ecological Conservation Redline program and the transfer of payments to areas with key ecological functions (Ren et al., 2015; Xu et al., 2022; Zhang et al., 2022), 21.4% of China's 7300 vertebrate species are threatened with extinction (Gong et al., 2020), which is higher than the world average (~20%).

China's largest national reserves are located in the provinces of Qinghai and Xizang, which account for 61.2% (881,280 km^2) of the total area of local and provincial reserves (1,440,000 km^2) and 75.3% of the total area of the National Nature Reserve system (1,175,040 km^2). This vast landscape includes 33.6% of China's mammals (Xu et al., 2017); however, only two or three primate species are present in these largest reserves (Li et al., 2018). China's primate species are present across 418 reserves (185 national-level and 233 provincial-level reserves) (Li et al., 2018), representing an area of 352,089.4 km^2, or approximately 22% of China's PAs (https://www.protectedplanet.net/country/CN). And, although these areas have played an important role in reducing deforestation and hunting within reserve boundaries, they have not had the same effect in areas adjacent to reserves (Ren et al., 2015). Moreover, despite the fact that China has set aside billions of dollars for reforestation (Li et al., 2018), most of these programs were not designed to regenerate or restore native habitats, which are crucial for primate survival.

To address these limitations and present a nation-wide focus, we analyzed and integrated the most comprehensive set of environmental data, including indicators of human activity, human population density (HPD, a measure of human impact on the natural environment), gross domestic product (GDP), roads, the normalized difference vegetation index (NDVI), location and size of PAs, and expected changes in temperature and rainfall, on the occurrence and future distribution of 26 primate species in China. For each species, we used ensemble species distribution models (SDMs) to predict how species' range distributions are expected to shift in response to future human activity, climate change, and modification in land cover (Biber et al., 2023; Li, Ru, et al., 2022; Mi et al., 2023; Pinto et al., 2023; Struebig et al., 2015). In the case of China, previous studies using SDMs were conducted on a single or a small number of species and relied on now outdated IPCC climate emission scenarios (Li, Chen, et al., 2022; Li, Ru, et al., 2022; Yu et al., 2022; Zhao et al., 2019, 2022). Our goals were to: (1) identify the most critical factors associated with human activities and climate change that impact the distribution of primate species in China; (2) assess the impact of human activities on the present and future availability of habitats suitable for primates; (3) assess the impact of climate change on present and future patterns of primate range shift; and (4) predict patterns of primate species diversity under current and future climate scenarios that include the effects of carbon dioxide emissions on changes in habitat suitability.

2 | MATERIALS AND METHODS

2.1 | Occurrence data

We obtained occurrence data for primates in China from the following sources: (1) published literature (Fan, 2012; Fan et al., 2017; Ji & Jiang, 2004; Li et al., 2018, 2022, the latest reports of Chinese primates, National Forest and Grassland Administration, 2009; Wei, 2022); (2) a database of the Catalogue of life China 2022 annual checklist (http://sp2000.org.cn/), the Global Biodiversity Information Facility (https://www.gbif.org/), and the IUCN Red List of Threatened Species (https://www.iucnredlist.org/), (downloaded data from 1970 to 2022 accessed in November 2022); and (3) our field survey records. If occurrence data from the published literature only included the place name, we then georeferenced the location names with Google Earth and sampled the place name according to the occurrence data, the description of the area from the published literature, and consulted with experts to determine whether the reported sample site was the actual site where the data were obtained. In total, we collected 10,378 occurrence records from the original literature and source information (Table S1: https://doi.org/10.5061/dryad.51c59zwfq). We removed the fewest number of points required to reduce the effects of geographic sampling bias using a hierarchical algorithm with 100 repetitions in spThin (R package) (Aiello-Lammens et al., 2015). After collation and screening, we used 7972 records for 26 primate species in China.

2.2 | Environmental predictors

We obtained bioclimatic variables from WorldClim (http://www.worldclim.org/). The WorldClim dataset provides bioclimatic data (Version 2.0, http://www.worldclim.org/) for 1970–2000 and future climate data (i.e., the 2050s: 2041–2060; 2070s: 2061–2080) with a 2.5′ spatial resolution. To determine future climate change, 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 the IPCC of the Intergovernmental Panel on Climate Change (Popp et al., 2017). Because it provides the best performance in East Asia, we selected the Beijing Climate Center Climate System Model (BCC-CSM2-MR) as developed at the National Climate Center (Wu et al., 2019). Scholars in China have typically used BCC-CSM2-MR to predict species distributions (Zhang, Liu, et al., 2021). SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 represent low, medium, medium-to-high, and high-forcing scenarios, respectively (Fischer et al., 2005). We selected SSP1-2.6 and SSP5-8.5 as representative of the minimum and maximum greenhouse emission scenarios, respectively, to predict the potential spatial distribution of primates in China. To overcome the problem of over-fitting caused by the multicollinearity of 19 climatic factors in the model results, we screened variables using the Spearman's correlation coefficient. If the value was >.8, it was omitted and deemed to be a highly correlated climate factor (Graham, 2003). Finally, we selected 13 bioclimatic variables to predict a primate species' potential range (Table S2). We also downloaded two commonly used indicators of the cumulative impact of human activity: HPD with a spatial resolution of 0.25 km^2 (http://sedac.ciesin.columbia.edu) and global human influence index (IGHP) with a spatial resolution of 0.25 km^2 (https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-ighp/data-download). Given that HPD was highly correlated with IGHP (Pearson r > .80), we only retained the HPD factors. We used PAs from the November 2022 World Database of Protected Areas dataset (https://www.protectedplanet.net/en#4_43.25_111_0), a resource widely used in conservation biology and biogeography studies related to PAs on a global scale (Mi et al., 2023), road (https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1/data-download), NDVI MOD13Q1 Version 6, with a spatial resolution of 0.25 km^2 (https://lpdaac.usgs.gov/products/mod13q1v006/), and the GDP of China with a spatial resolution of 0.25 km^2 (https://search.earthdata.nasa.gov/search). We also screened variables using the Spearman's correlation coefficient. If the value was >.8, it was omitted and deemed to be a highly correlated factor. Raster resolution varied between the bioclimatic and human activity data layers (0.25–1.00 km^2), so we resampled all layers to the resolution of the least fine raster (1.00 km^2) using the nearest-neighbor method in the "raster" package. These variables considered to have a major effect on primate ecology and range distribution, including bio 1, bio 3, bio 6, bio 12, bio 14, bio 15 (Li, Chen, et al., 2022), bio 1, bio 2, bio 4, bio 5, bio7, bio16, bio17, bio 18 (Li et al., 2023), bio 2, bio 4, bio 6, bio7, bio 16, bio 17 (Condro et al., 2021), bio 2, bio3, bio 5, bio 12, bio 17 (Schüßler et al., 2023), bio 4, HPD (Zhao et al., 2022), GDP (Estrada et al., 2020), and NDVI (Willems et al., 2009) also were examined (Table S2).

2.3 | Species distribution models

We used the "sdm" package in R (Voldoire et al., 2013) to implement an ensemble SDM to predict species distributions with a high-performance cluster. This was accomplished by inputting the occurrence data with climate and human activity factors to generate pseudoabsence records using the "gRandom" method (Voldoire et al., 2013). We then used a 75% random sample of initial data (presence–absence) as training data and evaluated this against the remaining 25% of the samples for each of the 26 primate species. We repeated the split sampling 10 times to account for the uncertainty associated with data partitioning (Mi et al., 2023). In sum, we used 16 commonly used high model performance SDM algorithms in the ensemble models: maximum entropy (MaxEnt) (Zhang et al., 2018), random forests (Williams et al., 2009), generalized additive model (Biber et al., 2023), generalized linear model, GLMPOLY, and GLMNET (Williams et al., 2009), support vector machine, Maxlike, multivariate adaptive regression spline, classification and regression trees (Naimi & Araújo, 2016), multilayer perceptron (Munoz-Mas et al., 2017), radial basis function (Aldossari et al., 2022), mixture discriminant analysis (Marmion et al., 2009), recursive partitioning and regression trees, flexible discriminant analysis (Mugo & Saitoh, 2020), DOMAIN (Mugo & Saitoh, 2020; Tsoar et al., 2007), and boosted regression trees (Elith et al., 2008). Then, we used true skill statistics (Allouche et al., 2006) and the values of the area under a receiver operating characteristic curve (AUC) to calibrate and validate the robustness of the evaluation using the 16 models (model selection) (Mi et al., 2023). The values ranged from 0.5 to 1, with high values implying high levels of model prediction accuracy (Table S2) (Zhang et al., 2018). Finally, we only selected a model if AUC and TSS were both high, and the model running results showed that both the AUC and TSS values for the MaxEnt model were higher than for any other model (Figures S1 and S2). Therefore, we only used MaxEnt models to predict species distributions (Mi et al., 2023; Zhang et al., 2018). In addition, we used MaxEnt models to analyze the normalized NDVI, GDP, tPA, roads, and HPD, with data on 26 primate species in China (Figure S3) (Gorczynski et al., 2022). This was done to identify the main factors affecting the availability and distribution of remaining suitable habitat for each species. To better understand the expected effects of climate change on the future availability of suitable habitats for primates, we modeled the distribution of potentially suitable habitats under four future climate scenarios using MaxEnt modeling (Figure S4) (Fan et al., 2015; Grueter et al., 2018; Korstjens et al., 2010; Shil et al., 2020).

Potentially suitable habitat maps for each species were transformed into binary distribution maps (presence/absence) using the threshold that maximizes TSS and AUC. This approach has been widely used in producing species distribution maps (Barbet-Massin et al., 2012; Mi et al., 2023). We transformed the output into a raster format using ArcMap 10.4 ArcGIS for further analysis.

The final map of each species' potential suitable habitat under human activities and the current climate had a range of values from 0 to 1. These were regrouped into four classes of potential habitats namely "highly suitable" (0.6–1), "moderately suitable" (0.4–0.6), "poorly suitable" (0.2–0.4), and "unsuitable" (<0.2) (Zhang et al., 2018). After using the current climatic data to model the spatial extent of suitable habitat for primate species in China, modeling projections were performed for four future climate scenarios (SSP1-2.6-2050s, SSP1-2.6-2070s, SSP5-8.5-2050s, and SSP5-8.5-2070s) to predict the extent of suitable habitat. The derived future habitat polygons were classified as "range expansion," "range contraction," and "no change". Subsequently, we estimated the spatial range for each of the three possible situations.

In addition, we superimposed a grid with 0.5° latitude/longitude cells (an area equivalent to 2300 km^2) of the current distribution area of each primate species. This totaled 1383 grid cells. The species richness for current and future scenarios was calculated as the number of species present in each grid cell. We also calculated the difference between future and current species richness. We calculated the distribution area of each species in the present and for expected scenarios in the future. We performed the analysis of species richness for all expected climate change scenarios (SSP2.6 and 8.5) (Condro et al., 2021; Lima et al., 2019).

3 | RESULTS

3.1 | The effects of human activities on changes in the current availability of primate suitable habitats

We found that the current distribution of primates in China is positively affected by NDVI (contribution of 54%) and the size of a PA (contribution of 19.1%), and negatively affected by the GDP (contribution of 21%) (Table S3). Thus, higher-income regions (>0 increase in GDP; Figure S3d) were characterized by increased environmental change and a reduction in the availability of suitable habitat for primates. Primate distributions were unrelated to HPD and road/rail density (Table S3). In addition, we found that areas of higher NDVI also were areas that contained a greater proportional increase in the availability of suitable habitat (NDVI ranged from 0.86 to 0.92). These areas of high habitat suitability were present principally in the core area of a reserve (defined as an area radiating out from the midpoint of each reserve for a distance of 0.1–0.5 km) and at a distance of 2.7–4.5 km outside the border of protected reserves (Figure S3c). Areas of lowest primate habitat suitability were found in non-PAs and areas inside PAs that had low NDVI values (<0.87; Figure S3a). These results highlight the importance of expanding PAs, reducing the human footprint in PAs, and constructing forested corridors that serve to connect previously isolated subpopulations in order to counteract the negative effects of forest fragmentation on primate survivorship.

We examined the currently available area of suitable habitat for each primate species. In general, based on NDVI, the current location of highly suitable primate habitats was principally distributed in southwestern, central, eastern, and southern China (Figure 1a; $73.28 \times 10^4 km^2$; Figure 1d). However, these habitats were highly fragmented (Figure 1a). The availability of moderately suitable habitat was mainly distributed in central, eastern, and southern China (Figure 1a; $76.67 \times 10^4 km^2$; Figure 1d). Further analysis indicated that within PAs, highly suitable habitats ($35.53 \times 10^4 km^2$; Figure 1d) and moderately suitable habitats ($156.23 \times 10^4 km^2$, Figure 1a,b,d)

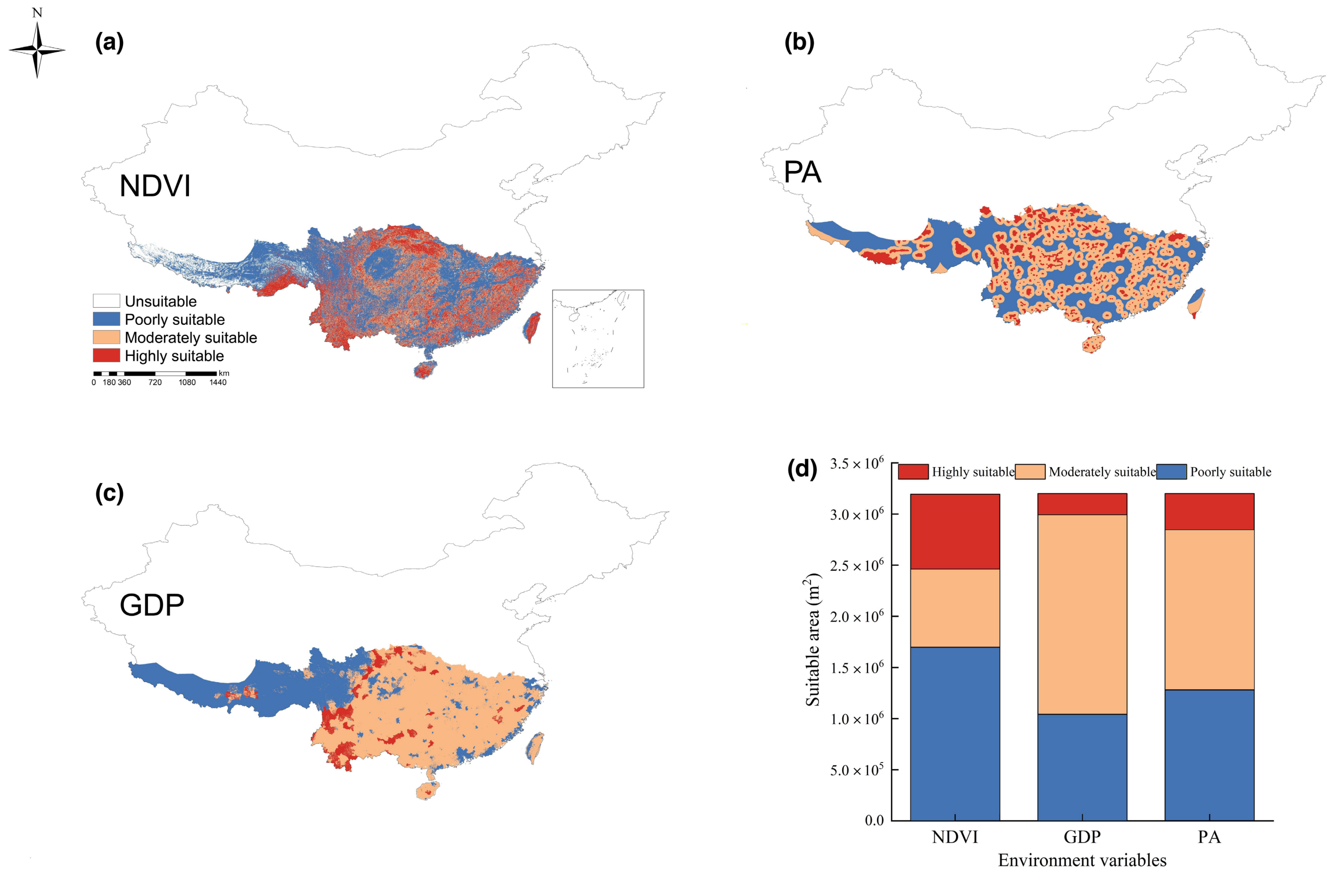

FIGURE 1 Current highly suitable, moderately suitable, poorly suitable, and unsuitable habitat distributions of 26 primate species in China. (a) Current potential distribution under the normalized difference vegetation index (NDVI); (b) current potential distribution under protected area (PA); (c) current potential distribution under gross domestic product (GDP); (d) current highly suitable, moderately suitable, poorly suitable, and unsuitable habitats, as well as the total distribution area under different environment variables. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

were mainly distributed in southwestern China (Figure 1b). Based on GDP, areas of highly suitable ($20.67 \times 10^4\,km^2$) and moderately suitable ($195.29 \times 10^4\,km^2$) habitat for primates were mainly concentrated in locations in southwestern, southern, and eastern China, whereas areas of poorly suitable habitat ($104.04 \times 10^4\,km^2$) were located in eastern coastal and western China (Figure 1c,d).

3.2 | The effect of climate change on primate current and future range shifts

The results indicated that expected changes in temperature (bio 1, 2, 3, 4, 7, 8, 9) and precipitation (bio 12, 14, 15, 16, 17, 18) contributed significantly to future primate's distributions; however, this varied considerably by species (Figure S4; Table S4).

Under current climate scenarios, the distribution of suitable primate habitats was similar to that of the present-day distribution of these habitats, suggesting that climate models can be used to accurately predict the potential future range of primates. We found that future areas of highly suitable primate habitats are expected to be concentrated in the southwestern (southeast Xizang, southwest Yunnan), southern (Hainan), and eastern regions of China (Anhui, Zhejiang, and Taiwan) ($4.02 \times 10^4\,km^2$). Areas of moderately suitable habitat will be distributed in southern, southwestern, and eastern China ($202.44 \times 10^4\,km^2$) (Figure 2a,b). However, based on current climate scenarios, most (98.74%) of the remaining areas available to primates will contain only moderately or poorly suitable habitat and therefore lead to additional population decline. Moreover, we found that the area of suitable habitat for primates is expected to decrease under future climate scenarios, and this trend will become more and more exacerbated over time (Figure 2). The models indicated that over the next 30 years, suitable habitat for primates would be distributed across small and widely scattered areas of southwestern (southeast Xizang, west Yunnan, south Guangxi), southern (Hainan Island), eastern (Taiwan, south Anhui), and central (Shaanxi, Chongqing) China (Figure 2). However, based on the projection using the lowest emission scenario (SSPI-2.6), by the year 2050, the amount of highly ($5.75 \times 10^4\,km^2$) suitable habitat ($119.87 \times 10^4\,km^2$) is expected to increase by 43.03%, and the amount of poorly suitable habitat is expected to increase by 5.57%. Moderately suitable area will decrease by 3.98% (to $194.38 \times 10^4\,km^2$; Figure 2c,b). For SSP5-8.5, projections indicate that highly suitable habitat will decrease by 8.46% (to $3.68 \times 10^4\,km^2$) and moderately suitable habitat will decrease by 6.15% (to $189.86 \times 10^4\,km^2$). In both models, poorly suitable habitat

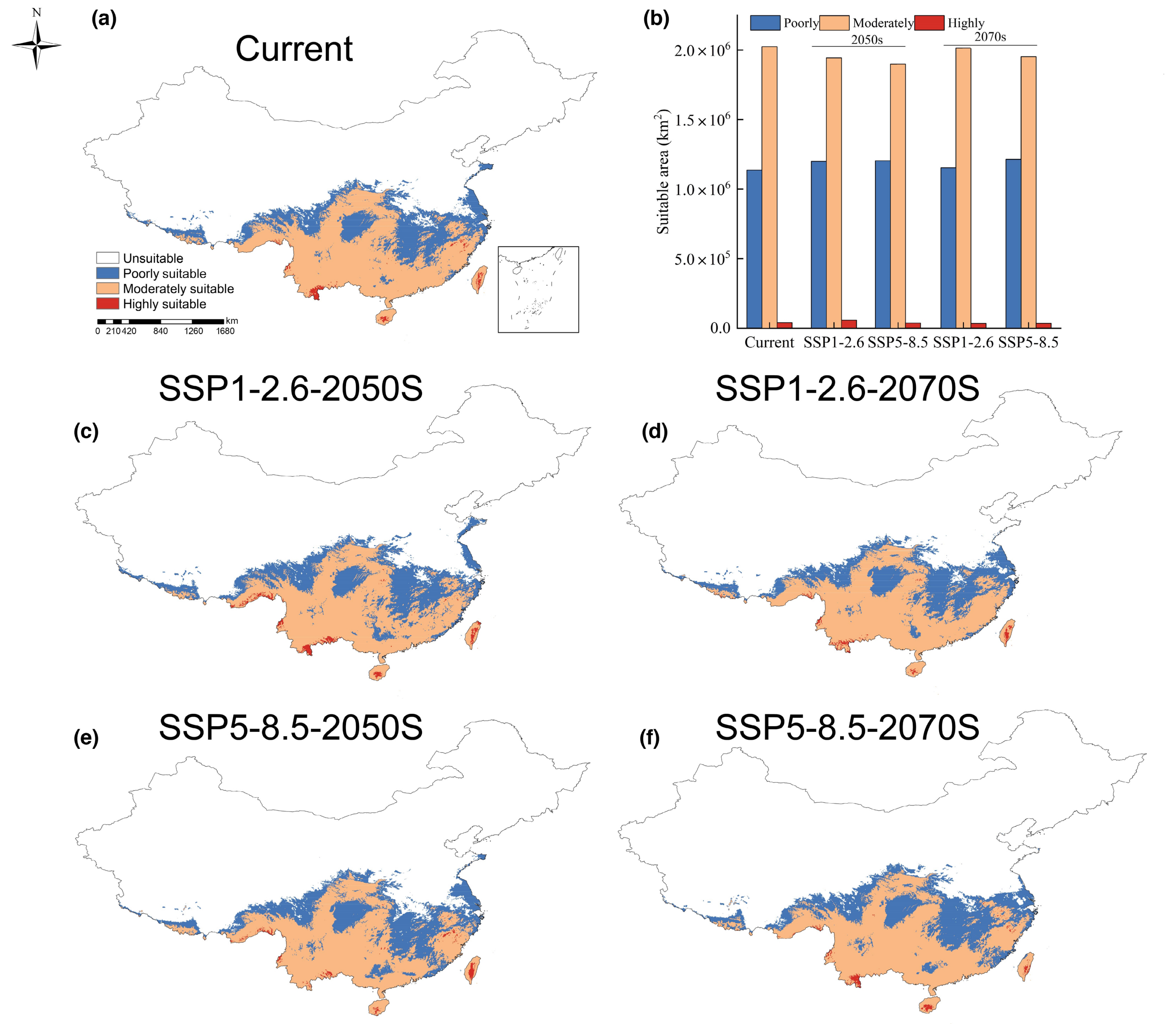

FIGURE 2 Future potential distribution of 26 primate species in China from 2050 to 2070. (a) Map of the potential suitable habitat for primates under current climate scenarios; (b) potential highly, moderately, and poorly suitable habitat for primates in the present and based on four future climate scenarios, SSP1-2.6 and SSP5-8.5 from the 2050s to the 2070s; (c) map of the potential suitable habitat for primates based on the SSP1-2.6 scenarios (2050s); (d) map of the potential suitable habitat for primates based on the SSP1-2.6 (2070s) scenario; (e) map of the potential suitable habitat for primates based on the SSP5-8.5 (2050s) scenario; (f) map of the potential suitable habitat for primates based on the SSP5-8.5 (2070s) scenario. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

will increase to $120.37 \times 10^4\,km^2$ (6.02%) compared with current climatic conditions (Figure 2b,e). This is expected to have a significantly negative effect on the distribution of 13 primate species in China, including: *Hoolock hoolock* (18.40%), *H. tianxing* (3.16%), *Nomascus hainanus* (14.21%), *Macaca assamensis* (10.60%), *M. cyclopis* (8.88%), *M. munzala* (8.53%), *M. mulatta* (1.02%), *Nycticebus bengalensis* (8.50%), *N. pygmaeus* (3.41%), *Rhinopithecus roxellana* (7.75%), *R. brelichi* (3.30%), *Trachypithecus shortridgei* (2.27%), and *T. melamera* (1.13%). Two of these species are listed by the IUCN as critically endangered, and eight are listed as threatened. Under scenario SSP1-2.6 (low CO_2 emission), potential highly suitable primate habitat will decrease by a minimum of 1.02% and a maximum of 18.40%. This is expected to negatively affect *H. hoolock*, *N. hainanus*, and *M. assamensis* (Figure S5; Table S5). Moderately suitable habitat will decrease by a minimum of 0.05% and a maximum of 18.41% for *R. strykeri* (18.41%), *R. roxellana* (2.97%), *M. thibetana* (15.91%), *M. arctoides* (13.43%), *N. hainanus* (12.43%), *N. concolor* (3.89%), *H. hoolock* (11.84%), *T. melamera* (2.42%), *M. leonina* (2.18%), *M. mulatta* (1.08%), and *M. munzala* (0.46%) (42.31%; 11/26; Figure S5; Table S5). In this model, poorly suitable habitat will decrease by a minimum of 0.07% and a maximum of 51.76% for *R. strykeri* (51.76%), *R. brelichi* (4.6%), *R. bieti* (2.48%), *N. hainanus* (33.91%), *N. concolor* (29.4%), *N.*

nasutus (29.0%), *Nycticebus. bengalensis* (9.09%), *H. hoolock* (6.91%), *M. assamensis* (6.25%), *M. munzala* (4.27%), *M. cyclopis* (0.07%), and *Nycticebus. pygmaeus* (4.99%) (46.15%; 12/26 species; Figure S5; Table S5). Under the high-forcing scenario (SSP5-8.5), potential highly suitable habitat will decrease by a minimum of 0.02% and a maximum of 32.03% for *H. hoolock* (32.03%), *H. tianxing* (0.09%), *N. hainanus* (9.69%), *R. strykeri* (22.57%), *R. roxellana* (1.53%), *R. brelichi* (3.03%), *Nycticebus pygmaeus* (19.03%), *N. bengalensis* (9.11%), *M. cyclopis* (12.23%), *M. arctoides* (3.64%), *M. mulatta* (3.46%), *M. assamensis* (5.86%), *Semnopithecus schistaceus* (8.05%), *T. melamera* (0.03%), and *T. pileatus* (0.02%) (57.7%; 15/26 species, 10 of which are listed as threatened; Figure S5; Table S5). Moderately suitable habitats are expected to decrease by a minimum of 0.05% and a maximum of 40.04% for *H. hoolock* (40.04%), *H. tianxing* (0.05%), *N. hainanus* (18.03%), *N. concolor* (2.48%), *M. thibetana* (18.04%), *M. arctoides* (16.63%), *M. leonine* (14.91%), *M. munzala* (11.35%), *T. shortridgei* (12.09%), *T. francoisi* (5.32%), and *R. bieti* (5.85%) (42.31%; 11/26 species, Figure S5; Table S5). Finally, potential poorly suitable habitat is expected to decrease (i.e., become unsuitable) by a minimum of 1.07% and a maximum of 37.7% for *H. tianxing* (14.01%), *H. hoolock* (8.88%), *N. hainanus* (36.83%), *N. concolor* (22.38%), *N. nasutus* (13.17%), *M. cyclopis* (37.70%), *M. munzala* (14.49%), *M. mulatta* (11.10%), *M. assamensis* (8.27%), *M. leonina* (5.31%), *T. shortridgei* (25.38%), *T. melamera* (12.41%), *T. francoisi* (1.07%), *R. bieti* (11.19%), *R. roxellana* (2.51%), and *N. bengalensis* (3.89%) (61.54%; 16/26 species; Figure S5; Table S5).

By the year 2070, climate models SSP1-2.6 and SSP5-8.5 predict that highly suitable areas for primates will total 3.37×10^4 km^2 and 3.45×10^4 km^2, and moderately suitable habitats will total 201.34×10^4 km^2 and 195.17×10^4 km^2, respectively (Figure 2b). This will result in a decrease of from 14.18% to 16.17% in highly suitable habitat and a decrease of from 0.25% to 3.6% in moderately suitable habitat from their current values. The area of poorly suitable habitat (115.29×10^4 km^2 and 121.39×10^4 km^2 under each of the two climate scenarios) is expected to increase from 1.54% to 6.9% (Figure 2b,d,f). Under both climate scenarios, by 2070, the potential spatial distribution of primates in China is expected to result in a major population decline. Under the low CO_2 emission scenario SSP1-2.6, potential highly suitable habitat will decrease by a minimum of 0.3% to a maximum of 67.25%. The primate species most severely affected include *R. strykeri* (67.25%), *R. roxellana* (67.25%), *H. hoolock* (12.32%), *H. tianxing* (9.22%), *N. nasutus* (28.09%), *N. hainanus* (18.11%), *M. arctoides* (11.92%), *M. assamensis* (2.38%), *M. mulatta* (2.14%), *M. leonina* (7.64%), *M. cyclopis* (6.08%), *N. bengalensis* (9.13%), *T. francoisi* (3.00%), *T. pileatus* (2.59%), and *T. shortridgei* (0.3%) (57.69%; 15/26) (Figure S5; Table S5).

Under the MaxEnt model, potential moderately suitable habitat is expected to decrease by a minimum of 1.7% to a maximum of 24.01% for *T. francoisi* (24.01%), *T. melamera* (22.55%), *T. leucocephalus* (19.15%), *T. shortridgei* (15.41%), *N. concolor* (11.01%), *H. hoolock* (5.74%), *M. munzala* (8.97%), *M. thibetana* (8.91%), *M. leonina* (5.06%), and *M. arctoides* (1.69%) (38.46%; 10/26 species; Figure S5; Table S5). Similarly, poorly suitable habitat is expected to decrease by a minimum of 0.6% and a maximum of 42.17% for species such as *N. hainanus* (42.17%), *N. concolor* (20.47%), *H. hoolock* (11.45%), *H. tianxing* (0.6%), *M. munzala* (19.06%), *M. thibetana* (13.62%), *M. assamensis* (13.15%), *M. cyclopis* (4.39%), *M. mulatta* (1.11%), *N. bengalensis* (14.81%), *T. francoisi* (10.21%), *T. crepusculus* (5.89%), *T. melamera* (2.43%), and *R. bieti* (7.70%) (53.85%; 14/26, Figure S5; Table S5). Under the high-forcing scenario (SSP5-8.5), potential highly suitable habitat will decrease by a minimum of 0.98% and a maximum of 56.91% for *R. strykeri* (56.91%), *R. brelichi* (7.88%), *H. tianxing* (26.98%), *H. hoolock* (15.90%), *N. hainanus* (14.33%), *N. bengalensis* (15.61%), *N. pygmaeus* (9.74%), *T. pileatus* (8.97%), *T. melamera* (3.94%), *T. shortridgei* (2.56%), *T. crepusculus* (0.98%), *M. arctoides* (7.44%), *M. cyclopis* (5.58%), *M. mulatta* (2.46%), and *M. assamensis* (1.36%) (57.69%; 15/26; Figure S5; Table S5). The availability of moderately suitable habitat will decrease by a minimum of 0.20% and a maximum of 29.70% for *N. nasutus* (29.70%), *N. hainanus* (21.48%), *N. concolor* (14.83%), *H. tianxing* (19.98%), *H. hoolock* (8.23%), *M. thibetana* (27.73%), *M. arctoides* (6.07%), *M. leonina* (4.07%), *R. brelichi* (23.61%), *T. shortridgei* (6.22%), *T. melamera* (4.05%), and *T. francoisi* (0.20%) (46.15%; 12/26; Figure S5; Table S5). Finally, poorly suitable habitat is expected to decrease, and therefore not be used by primates, by a minimum of 0.88% to a maximum of 56.39% for *N. concolor* (56.39%), *N. hainanus* (44.07%), *N. nasutus* (43.75%), *H. tianxing* (31.95%), *H. hoolock* (12.50%), *R. brelichi* (29.36%), *R. bieti* (4.23%), *R. roxellana* (0.88%), *M. assamensis* (22.80%), *M. leonina* (15.00%), *M. thibetana* (5.15%), *M. mulatta* (4.29%), *N. bengalensis* (14.85%), *N. pygmaeus* (10.78%), and *T. francoisi* (7.61%) (57.69%; 15/26 species; Figure S5; Table S5).

The results indicate that under four future climate scenarios (SSP1-2.6-2050s, SSP1-2.6-2070s, SSP5-8.5-2050s, and SSP5-8.5-2070s), there will be range expansion (from 6.25×10^4 km^2 to 9.95×10^4 km^2; Figure S6; Table 1) and range contraction for individual primate species (from 5.6×10^4 km^2 to 10.93×10^4 km^2; Figure S6;

TABLE 1 Projected range expansion, range contraction, and no distributional change for primates in China[a] under four future climate scenarios in China.

SSPs	Range expansion ($\times10^4$ km^2)	Range contraction ($\times10^4$ km^2)	No change ($\times10^4$ km^2)
SSP1-2.6-2050s	7.31	5.6	36.43
SSP1-2.6-2070s	6.25	8.09	35.65
SSP5-8.5-2050s	9.95	7.01	35.09
SSP5-8.5-2050s	7.54	10.93	34.02

[a]Note that these changes in range distribution do not indicate whether range expansion or range contraction occur in areas of highly suitable, moderately suitable, or poorly suitable habitat.

Table 1). Habitat expansion is expected to be concentrated in the central, southwestern, and southern regions of China (Figure S6; Table 1), and habitat contraction is expected to be concentrated in eastern, central, and southwestern China. The model indicated that over the next 30–50 years under the low CO_2 emission scenario SSP1-2.6, the potential suitable habitat for *N. hainanus* (from 0.00 km^2 to 0.32 × 10^4 km^2), *N. concolor* (7.50 × 10^4 km^2 to 31.18 × 10^4 km^2), *H. hoolock* (0.63 × 10^4 km^2 to 17.21 × 10^4 km^2), *R. strykeri* (0.04 × 10^4 km^2 to 0.45 × 10^4 km^2), *R. brelichi* (3.51 × 10^4 km^2 to 24.82 × 10^4 km^2), *R. roxellana* (13.39 × 10^4 km^2 to 15.27 × 10^4 km^2), *M. munzala* (1.30 × 10^4 km^2 to 4.45 × 10^4 km^2), *M. assamensis* (26.65 × 10^4 km^2 to 61.69 × 10^4 km^2), *M. mulatta* (65.25 × 10^4 km^2 to 71.25 × 10^4 km^2), and *N. pygmaeus* (0.82 × 10^4 km^2 to 2.02 × 10^4 km^2) will expand (Figure S7; Table S6). Under the high-forcing scenario SSP5-8.5, the potentially suitable habitat for *N. hainanus* (0.00 km^2 to 0.01 × 10^4 km^2), *H. hoolock* (0.51 × 10^4 km^2 to 38.11 × 10^4 km^2), *H. tianxing* (1.84 × 10^4 km^2 to 2.32 × 10^4 km^2), *R. roxellana* (18.16 × 10^4 km^2 to 26.45 × 10^4 km^2), *R. bieti* (3.43 × 10^4 km^2 to 9.05 × 10^4 km^2), *R. strykeri* (1.10 × 10^4 km^2 to 1.40 × 10^4 km^2), *M. cyclopis* (0.10 × 10^4 km^2 to 0.41 × 10^4 km^2), *M. munzala* (1.90 × 10^4 km^2 to 7.22 × 10^4 km^2), *M. mulatta* (30.19 × 10^4 km^2 to 106.69 × 10^4 km^2), *M. arctoides* (50.69 × 10^4 km^2 to 76.52 × 10^4 km^2), *M. assamensis* (34.67 × 10^4 km^2 to 51.23 × 10^4 km^2), *T. melamera* (0.15 × 10^4 km^2 to 0.59 × 10^4 km^2), *T. crepusculus* (8.46 × 10^4 km^2 to 11.69 × 10^4 km^2), and *T. shortridgei* (0.17 × 10^4 km^2 to 0.22 × 10^4 km^2) is expected to expand (Figure S7; Table S6). However, our analysis does not allow us to determine whether that expansion will principally occur in areas of poorly suitable habitat, moderately suitable habitat, or highly suitable habitat. Overall, this suggests that as climate warming intensifies, the potentially available suitable habitat for several primate species in China is expected to expand from 38.46% (10/26) for SSP1-2.6 to 53.85% (14/26) for SSP5–8.5 (Figure S7; Table S6).

3.3 | The effect of climate change on primate current and future spat-temporal diversity

Patterns of primate species richness were found to vary among regions, ranging from one to nine species per grid cell (Figure 3a). The grid cells with high species richness were concentrated in the biodiversity hotspots of southwest China (Yunnan, 9 species per grid cell; Guangxi, 6–8 species per grid cell; Sichuan and Guizhou, 4–5 species per grid cell; Figure 3a). Projections for the years 2050 and 2070 revealed that all regions are expected to face a reduction in the number of species (Figure 3b). Under the low CO_2 emission scenarios SSP1-2.6, over the next 30 years, 25.0% (346/1383) of grid cells are expected to lose 1–6 species and 1.8% will be lost ($n = 26$ grid cells) 3–6 species. In contrast, 25.1% (348/1383) of grid cells will gain 1–4 species, and 1.2% (17 grid cells) are expected to gain 3–4 species (Figure 3b). However, this simply represents a redistribution of species. For the purposes of conservation, six species are expected to be lost from Yunnan Province, four species will be lost from the provinces of Guangxi and Guizhou, and three species will be lost in Xizang (Figure 3b,c). In the next 50 years, 23.64% (327/1383) of grid cells will lose 1–5 species, and 2.6% (36 grid cells) are expected to lose 3–5 species. During this same period, 29.79% (412/1383) of grid cells will gain 1–4 species, and 0.6% (9 grid cells) are expected to gain 3–4 species (Figure 3b). Overall, five species will be lost from Yunnan Province, four species each will be lost from Guangxi and Guangdong Provinces, and three species will be lost from Xizang (Figure 3b,d). Under the high-forcing scenarios SSP5-8.5, over the next 30 years, 23.8% (329/1383) of grid cells will lose 1–7 species and 2.1% (30 grid cells) will lose 3–7 species. In contrast, 27.9% of grid cells will gain 1–4 species, and 0.9% (13 grid cells) are expected to gain 3–4 species (Figure 3b). Under this model, seven species will be lost from Yunnan Province, five species will be lost from Guangxi Province, four species from Guangdong Province, and three species will be lost in Xizang (Figure 3b,e). Extending this to the next 50 years, 24.15% (334/1383) of grid cells will lose 1–5 species, and 2.0% (28 grid cells) will lose 3–5 species. This model also predicts that 32.6% (451/1383) of grid cells will gain 1–4 species, and 0.9% (13 grid cells) are expected to gain 3–4 species (Figure 3b). In total, five species will be lost from Yunnan, four from Guangxi, and three from Guangdong (Figure 3b,f). Our results found that areas of high primate richness are the most vulnerable to highly suitable habitat loss, and by the year 2070, the number of wild primate species in China will decline from 26 to 19.

4 | DISCUSSION

A comprehensive understanding of the effects of human activities and climate change on the distribution and richness of primates in China is essential for developing and implementing effective conservation measures and promoting the recovery and return of endangered wild populations (Li et al., 2022; Stewart et al., 2020; Yu et al., 2022). In China, most primate taxa are considered flagship species and play an important role in forest regeneration and maintaining ecosystem balance (Li et al., 2018). However, these same species are threatened by a long history of habitat conversion and are facing the future effects of climate change (Li, Chen, et al., 2022; Zhang, Turvey, Chapman, & Fan, 2021; Zhao et al., 2022; Zhao, Garber, et al., 2021). Since its founding some 70 years ago, China has experienced the largest and fastest process of internal migration and urbanization in world history. Some 914.25 million people (growth rate of +1.36% per year) (National Bureau of Statistics of China (Login acquisition date: October 24, 2023, Tuesday: http://www.stats.gov.cn/), or 64.7% of China's permanent population, now reside in cities. Correspondingly, China's rural population, which totals 498.35 million (a growth rate of −2.24% per year), has declined dramatically. At present, however, there is no comprehensive data set available from which to assess whether a reduction in the number of people living in rural areas that coincide with primate ranges is having a positive or negative impact on the conservation of primate species.

Understanding the impact of current human conservation policies (creation and expansion of PAs, construction of corridors for

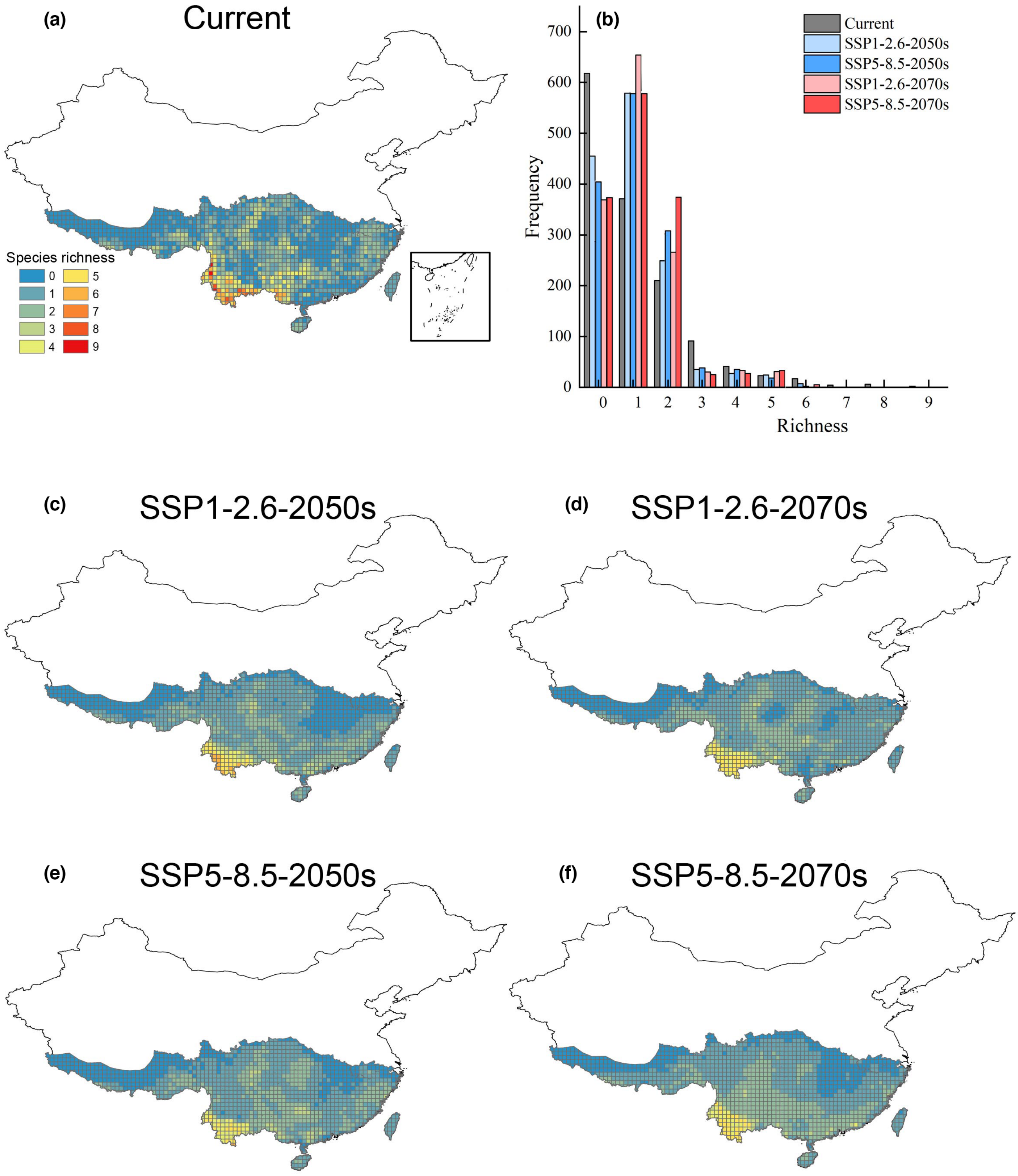

FIGURE 3 The impact of climate change on the spatial distribution of primate species richness in China. Primate species richness in the current and future climate scenarios SSP1-2.6 and SSP5-8.5. (a) Map of primate species richness under current climate scenario conditions; (b) histogram shows the frequency of cells with different primate species richness values under the present and future climate scenarios; (c) map of primate species richness based on the SSP1-2.6 climate scenario (2050s); (d) map of primate species richness based on the SSP1-2.6 (2070s) climate scenario; (e) map of primate species richness based on the SSP5-8.5 (2050s) scenario; (f) map of primate species richness based on the SSP5-8.5 (2070s) scenario. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

species migration and gene flow, and habitat restoration), economic policies (GDP), and climate on current and future distribution is widely regarded as one of the most important challenges needed to safeguard biodiversity (Mi et al., 2023). Our findings indicate that areas characterized by high levels of forest cover (NDVI) and the creation of government-sanctioned PAs, such as China's Natural Forest Protection Program and the National Nature Reserve Program, have had a positive impact on the distribution of primates in China (Figure 1a,b). These programs need to be expanded, however, given that over 80% of Chinese primate species are threatened with extinction (Li et al., 2018). Additionally, we found that areas immediately adjacent to the boundary of many PAs contain suitable habitat for primates (Figure S3c). Thus, extending the boundaries of PAs represents a critical conservation tool available to protect animal and plant biodiversity in China, including primates. Using SDMs, we found that factors such as temperature and annual precipitation have an important influence on primate distributions and the availability of suitable habitat (Figure S4). Our models indicate that under all future climate scenarios, the availability of highly suitable habitat for primates is expected to decrease, resulting in a decrease in species richness. In particular, primate species such as *Hoolock hoolock*, *R. strykeri*, *R. brelichi*, *Nycticebus pygmaeus*, *M. arctoides*, and *S. schistaceus* are expected to be lost from regions considered ecological hotspots such as Yunnan, Guizhou, Xizang, and Guangdong Provinces (Figure 3). However, we note that SDMs are always simplifications of extremely complex and unpredictable processes, and the resulting projections need to be interpreted with great caution.

Our study revealed that solutions to the primate extinction crisis in China require a dedicated national effort designed to restore native habitat and the immediate construction of natural and human-made corridors to connect isolated species subpopulations and expand the network of PAs (Figure 1a,b; Figure S3). PAs can effectively deter deforestation and hunting and facilitate the natural restoration of fragmented and impacted forests (Li, Chen, et al., 2022; Ren et al., 2015; Xu et al., 2022; Zhang, Turvey, et al., 2021). It is important to point out that habitat expansion is not the same as habitat connectivity. Virtually all primates in China are distributed in fragmented landscapes (with low landscape connectivity) and have limited opportunities for gene flow across subpopulations (Li et al., 2018; Zhao et al., 2019). Climate change may further increase habitat fragmentation and decrease connectivity in response to extreme weather events and raising temperatures (Stewart et al., 2020). Thus, in the absence of increasing habitat connectivity, the extinction risk for primates in highly fragmented landscapes remains high (Li et al., 2018; Stewart et al., 2020; Zhao et al., 2019). China has almost 12,000 PAs, covering approximately 20% of its land surface (Xu et al., 2019). We recommend that the area be increased to 30%. Given that areas located within 2.7–4.5 km of the boundary of PAs were found to contain suitable habitat for primates (Figure S3c), including these forests in the national protected reserve system would have high and immediate conservation benefits.

Most PAs in China are concentrated in mountainous regions such as Qinghai and Xizang, which account for 75.3% of the National Nature Reserve system and 33.6% of China's mammalian habitats (Xu et al., 2017). However, there are few primate species that inhabit these reserves (Li et al., 2018). In addition, two recent studies have suggested that PAs are unlikely to serve as stepping stones for species undergoing climate-induced range shifts (Parks et al., 2023; Xu et al., 2022), as management practices in these PAs are not sufficiently flexible to adapt to and anticipate species requirements under changing conditions or have the legal authority to expand PA boundaries (Parks et al., 2023; Xu et al., 2019, 2022). For example, a recent study reported that 16 of the 104 groups of critically endangered western black crested gibbons (*Nomascus concolor*) are located nearby but outside of the Wuliangshan National Nature Reserve in Yunnan, China (Fan et al., 2022). A similar situation exists for species such as François' Langurs (*Endangered*) (Zhou & Huang, 2021), golden snub-nosed monkeys (*Endangered*) (Yu et al., 2022), and Tibetan macaques (*Near Threatened*) (Li, Yang, et al., 2022), with many populations ranging outside of PAs. Thus, there is an imperative to expand the national system of PAs in China to safeguard threatened populations and species (Li et al., 2018).

We also found that primate habitat suitability decreases with increasing GDP (>0; Figure S3), indicating that areas of increased human development and infrastructure are not compatible with primate persistence (Estrada et al., 2022). It is worth noting that most areas of remaining highly suitable habitats for primates are located in economically underdeveloped areas of China (Figure 1c), with 80% of China's impoverished counties located in remote areas, whose natural ecosystem functions quickly degenerate in that of anthropogenic stresses (i.e., ecologically fragile areas) are considered ecologically fragile (Deng et al., 2016; Ma et al., 2022). Our results indicated that the majority of primate species are distributed in impoverished counties, especially in the southwest mountainous of China (Figure 1c). Given that hunting and logging have negative effects on primate survivorship (Ma et al., 2022; Zhao, Li, et al., 2021), effective conservation strategies to protect China's primates also must include social and economic policies that provide members of rural communities with increased food and economic security and culturally appropriate resources and incentives to maintain and protect wild primate populations.

Although different primates have different habitat requirements, according to the latest assessment report on the endangered status of primates in China, all primates depend on forests for shelter and prefer habitats such as evergreen broad-leaved forests, deciduous forests, and mixed forests of evergreen and deciduous trees (Table S7). It is inevitable that they will also inhabit areas with more intensive human activities. Almost all primates are facing the impacts of habitat fragmentation and human activities, such as road construction, grazing, and crop expansion (Table S7). Eighteen of China's 26 primate species have remaining populations of less than 3000 individuals, including species with less than 100 individuals (Hainan gibbons, pygmy slow loris) and several with less than 500 individuals (Guizhou snub-nosed monkeys, skywalker gibbon, and Hainan gibbon) (Table S7), and two other gibbon species have been extirpated from China in the past 20 years (Li et al., 2022). Therefore, this study integrated factors related to human activities to analyze the human threats faced by all primates, and the results are relatively reliable.

Our study found that extreme variation in annual temperature and lower precipitation were the main climate factors expected to result in primate species range reduction (Figure S3). With continued greenhouse emissions, temperatures are expected to increase, which will result in an increase in the intensity of extreme weather events. This is expected to bring new survival challenges to primates in China (Duffy et al., 2022; Sun et al., 2022; Zhang et al., 2019). The resulting droughts, floods, and extreme heat events that have already begun to occur in southwest China and along the coastal areas of southeastern China (Yu & Zhai, 2020) (Figure 2a) are expected to increase the extinction risk of primates moving forward. In order to mitigate the impact of extreme climate events on Chinese primates, special attention must be paid to protecting and expanding primate habitats in the southwestern regions of China.

In addition, studies have shown that climate change may increase forest fragmentation, dividing large areas of highly suitable habitat into small and disconnected habitats (Stewart et al., 2020). We found that the availability of potential highly suitable habitat will gradually decrease (Figure 2; Table 1). Virtually all primate species in China currently live in fragmented landscapes (with low landscape connectivity) and have a highly insular distribution, resulting in limited opportunities for gene flow (Li et al., 2018; Zhao et al., 2019). Primate dispersal across highly fragmented landscapes is limited (Anderson et al., 2007; Carvalho et al., 2019; Gouveia et al., 2016) and puts dispersing individuals at increased risk of being hunted, road mortality, disease, and capture (Boonratana, 2020; Marsh & Chapman, 2013). Further habitat fragmentation will continue to divide populations, increase dispersal distances between groups, lead to a reduction in genetic diversity, and accelerate population decline (Marsh & Chapman, 2013; Pinto et al., 2023).

Finally, we found that expected future climate change and land conversion will reduce Chinese primate richness over space and time (Figure 3). Currently, areas of high primate richness in China are concentrated in four neighboring provinces in the west and southwest (Yunnan, Guangxi, Xizang, and Guizhou) (Figure 3a). This region of China has witnessed its worst drought in nearly a decade, negatively impacting biodiversity, livestock, and the livelihoods of local residents (Li et al., 2018, 2022; Qiu, 2010).

In summary, our study found that primates in China will continue to be severely impacted by human activity and future climate change. These impacts are projected to have a considerable effect on the extent and location of species' geographical ranges and the availability of suitable habitat. Thus, to prevent large-scale declines in primate richness, it is crucial that China, the US, EU, and other industrial countries dramatically and immediately lower CO_2 emissions and that China expand PAs in regions and habitats with wild primate populations (Biber et al., 2023; Li et al., 2018; Zhang et al., 2022; Zhao et al., 2022).

AUTHOR CONTRIBUTIONS

Wen-Bo Li: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Yang Teng:** Formal analysis; investigation; methodology; software. **Ming-Yi Zhang:** Formal analysis; investigation; methodology; software. **Ying Shen:** Formal analysis; investigation; methodology; software. **Jia-Wen Liu:** Data curation; visualization. **Ji-Wei Qi:** Data curation; visualization. **Xiao-Chen Wang:** Data curation; visualization. **Rui-Feng Wu:** Data curation; visualization. **Jin-Hua Li:** Data curation; visualization. **Paul A. Garber:** Conceptualization; resources; supervision; writing – original draft; writing – review and editing. **Ming Li:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.51c59zwfq. These data were derived from the following resources available in the public domain: a database of the Catalogue of life China 2022 annual checklist (http://sp2000.org.cn/), the Global Biodiversity Information Facility (https://www.gbif.org/), the IUCN Red List of Threatened Species (https://www.iucnredlist.org/), accessed in November 2022; WorldClim (http://www.worldclim.org/); HPD (http://sedac.ciesin.columbia.edu); and the global human influence index (https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-ighp/data-download). PAs from the November 2022 World Database of Protected Areas dataset (https://www.protectedplanet.net/en#4_43.25_111_0), road (https://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1/data-download), normalized difference vegetation index MOD13Q1 Version 6 (https://lpdaac.usgs.gov/products/mod13q1v006/), gross domestic product of China (https://search.earthdata.nasa.gov/search).

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SUPPORTING INFORMATION

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