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Deduced Conservation Strategy of the Macaques in China from their Evolutionary Development

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Understanding how climate, ecological and environmental changes, and anthropogenic activities have driven animals' development and predicting their prospective distribution profiles are essential to making a tangible conservation strategy. Macaques (*Macaca*) distributed in China provide an ideal research model for such an effort. We reconstruct their geographic distribution profiles from the last inter-glaciation (LIG, 120,000–140,000 years BP), the Last Glacial Maximum (LGM, 22,000 years BP), and the present (1970–2000), based on which we deduce their distribution perspective in the 2050s. The results show that their suitable habitats during LIG and LGM were mainly in eastern Southwest, Central, and Coastal China. A noticeable distribution reduction started in LIG and persisted until the present (1970–2000). Their distribution centroid would shift northward to mountainous regions, mainly in Southwest China, where more migration corridors would be available for their prospective development. Also, the results indicate that China's Protected Area currently does not cover more than 94.00% of macaques' potential habitats, which is a dismal situation for their conservation. Finally, this study proclaims that the conservation priority of the macaques in the years to come should focus on Southwest China – their future refuge region.

Key words: Macaques' historical distribution, Climate Change, Human-induced activities, MaxEnt, Conservation model

BACKGROUND

Over the years, global climate, ecological changes, and environmental devastation triggered by human-induced activities have increased dramatically worldwide (Ofori et al. 2017; Measey et al. 2019). Thus, we are now facing enormous pressures driving geographic distribution patterns of plants and animals (Behroozian et al. 2020; Gainsbury 2020), altering ecological community structure (Zhou et al. 2017), and impacting ecosystem stability (Karimi et al. 2021). Such threats have led to significant animal migration, extinction, and population reduction (Chen et al. 2011; Hoffmann and Sgrò 2011), resulting in more than 75%

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alteration in contemporary terrestrial ecosystems (Venter et al. 2016), including extensive agricultural changes and deforestation (Gries et al. 2019) and accelerated expansion of urbanization (Jackson et al. 2001; Chen et al. 2002; Ellis et al. 2013; Eötvös et al. 2018; Duncan et al. 2020).

Thus, climate and ecological changes and human-induced activities, particularly geographic alterations, have created unprecedented diversity and conservation pressures (Worm et al. 2006; D'Agata et al. 2016). Changes in species' geographical range result in compelled migration towards suitable habitats, while some species cannot respond rapidly, being pushed to extinction (Radchuk et al. 2019; Doherty et al. 2021). For example, mountain lions exhibited significant antipredator behavior changes in response to habitat alteration, resulting in a 34% reduction in their distribution (Suraci et al. 2019), forcing them to abandon lower-risk home ranges (Schuette et al. 2013). Such combined impacts in the 21st century and beyond will further alter animals' distribution, causing the extinction of many wildlife species in the Sixth Mass Extinction (Struebig et al. 2015; Gouveia et al. 2016). Such phenomena especially apply to nonhuman primates, which are more sensitive to climate change and entirely dependent on forested ecosystems (Estrada et al. 2017; Zhang et al. 2019b), so that over 60% of extant global primate species are on the edge of extinction (Estrada et al. 2017; Carvalho et al. 2019). In China, such a scenario is even worse – approximately 80% of the 28 primate species are threatened (Li et al. 2018).

The macaques (*Macaca*) in the subfamily Cercopithecinae have 23 species in Africa and Asia (Roos et al. 2019). Their dispersal scenarios from Africa to Asia were driven by the environmental changes in the Miocene (Zinner et al. 2013; Roos et al. 2014): they originated in Africa and migrated to Europe and Asia following the collision of the Afro-Arabian plate with Eurasia during the Oligocene-Miocene (23.8–18 Mya). This collision created a land connection between Arabia and Southwest Asia, enabling many animal taxa, including macaques, to migrate from Africa to Asia via Europe. In other words, macaques' evolutionary development and distribution patterns have been remarkably driven by climate, ecological, and geographic changes since the Miocene. Except for the Barbary macaques (*Macaca sylvanus*) left in North Africa, the other macaque taxa reached southern East Asia in the Pliocene. They continued distributing to East and South Asia through alternative dispersal paths (Fig. 1; Li et al. 2020; Zhang et al. 2022). Seven extant species are now distributed in mainland China: rhesus macaques (*Macaca mulatta*), the northern pig-tailed macaque (*M. leonine*), the stump-tailed macaque (*M. arctoides*), the Assamese macaque (*M. assamensis*), the Tibetan macaque (*M. thibetana*), the Arunachal macaque (*M. munzala*), and the white-cheeked macaque (*M. leucogenys*). They all belong in Class II or I of Nationally Protected Wildlife in China. Seven are listed on the IUCN Red List of Threatened Species (IUCN 2022). The white-cheeked macaque, a recently discovered species (Li et al. 2015), is ranked as a Critically Endangered taxon according to the Red List of China's Vertebrates (Jiang et al. 2016). Thus, the conservation of macaques in China faces a significant challenge (Li et al. 2020; Huang et al. 2021).

Establishing dynamic spatial-temporal distribution models which reference climate alterations, vegetation types, geological features, anthropogenic activities, and evolutionary changes for macaques are necessary to make a tangible conservation strategy for these species, especially in predicting their distribution and survival prospects. Such a model would allow us to identify appropriate conservation measurements in advance. Macaque species (*Macaca*) found in China, including fossil and extant taxa, and their distribution profiles from the Pleistocene to the present, can provide ideal materials for such an endeavor. The Chinese fossil record includes two cercopithecine genera, *Procynocephalus* and *Macaca*. Both emerged in the Late Pliocene or Early Pleistocene, but only *Macaca* survived the Quaternary and is widely distributed (Pan and Jablonski 1987).

As for their conservation, some studies based on a few environmental and ecological variables were made on *M. assamensis* (Regmi et al. 2018; Khanal et al. 2019), *M. leonina* and *M. mulatta* (Sun et al. 2020). Those studies, which rely on current environmental and ecological parameters and consider the contemporary distribution profiles alone, likely offer limited information on dynamic information to identify drivers of their early declines leading to their current reduced population status. On the other hand, database-driven mathematical models are considered more tangible in making or amending conservation strategies (Zhang et al. 2022; Li et al. 2022). They allow us to scientifically prepare conservation plans and arrangements according to animals' prospective distribution trajectories.

Thus, this study's aims include 1) using the variables relevant to the changes in the environment, climate, ecology, geography, and human-induced activities to establish models reconstructing macaques' past, current, and future suitable habitat distribution patterns; 2) identify the significant factors driving such changes; and 3) establishing a database-driven conservation model for macaques, providing solid evidence for formulating their conservation perspective.

MATERIALS AND METHODS

Data of macaques and variables

This project includes datasets of geographic distributions of the fossil macaques found in the Pleistocene, including *Macaca youngi*, *M. jiangchuanensis*, *M. anderssoni*, *M. mulatta*, *M. robustus*, and *M.* spp., which are collectively illustrated in figure 1, and seven extant species in mainland China – *M. mulatta*, *M. arctoides*, *M. leonine*, *M. assamensis*, *M. thibetana*, *M. munzala* and *M. leucogenys*. They were collected from a broad literature review of academic journals, government annals, archives, magazines, and books in Chinese (Please see the details in Supplementary materials). Unfortunately, it is difficult, if not impossible, to define the relationship between fossil taxa and extant crown species – they are extensively overlapped in distribution, so all the taxa were analyzed at the genus (*Macaca*) rather than the species level.

Nineteen variables relevant to climatic, ecological, and environmental alterations, *Bioclimatic variables* (BC), were extracted from the WorldClim database (Fick and Hijmans 2017), which have been regarded to drive animals' geographic distribution and evolutionary development significantly (Virkkala and Lehikoinen 2017), especially regarding mammals (Sharma et al. 2019). As addressed above, like other catarrhines (colobines and apes) in Asia, macaques in East Asia started continental dispersion and radiation in the Late Miocene and Early Pliocene, about 5–6 Mya (Fig. 1), from Western China (Li et al. 2020). Severe climate changes drove such processes during the glaciation of the Quaternary (Otto-Bliesner et al. 2006; Li et al. 2020). Thus, to have an integral comprehension of distribution changes from the Pleistocene, the blooming period of the Asian macaques (Zhang et al. 2022), the fossil distribution of the macaques shown in figure 1 was also analyzed.

We used the shared socioeconomic pathways (SSPs) to analyze BC variables to predict the

Fig. 1. Illustration of the Asian macaques' reaching southwest East Asia during the Pliocene, after migrating from Africa, and their dispersal routes in Southeast and East Asia, which are modified according to (Li et al. 2020; Zhang et al. 2022). It illustrates the entrance of the Convergence-Divergence Center (CDC), dispersion along three major rivers in China, and migration through the landbridges along the coastal lines formed during the glaciation in the Pleistocene.

prospective distribution profile in the 2050s. Such a method has successfully been applied in predicting global temperature changes, referring to different trajectories and greenhouse gas (GHG) parameters in the 21st century (Riahi et al. 2017). Two different SSPs were considered – SSP5, assuming continuous accelerated GHG emissions, and SSP2, presuming a moderate emission level following the proposed reduction of GHG emissions (Riahi et al. 2017).

Land use variables (LU) were from Land-use Harmonization (https://luh.umd.edu/data.shtml), a database of LUH2 v2h covering 850–2015, and a future land-use dataset (LUH2 v2f) for CMIP6, including the period 2015–2100 (Hurtt et al. 2011). Considering the consistency of climate scenarios, we used SSP2 and SSP5 in this study. We analyzed eight variables for 1970–2000 and 2041–2060 to demonstrate the current and future distribution models for the 2050s.

The human population variables (HP) were downloaded from Spatial Population Scenarios for all five SSPs with decadal intervals and 0.125-degree resolution (Jones and O'Neill 2016). We obtained population distribution data for 2000 and proposed the two scenarios (SSP2 and SSP5) to calculate population density and distribution in the 2050s.

Periodic distribution models

1) The Last Interglacial Period (LIG, ~140,000–120,000 years ago). It was marked by modern humans (*Homo sapiens*), started the noticeable expansion and impacted upon environments (Hershkovitz et al. 2018; Harvati et al. 2019), which have since progressively accelerated (Cavalli-Sforza et al. 1993). 2) The Last Glacial Maximum (LGM). It was the period when the glaciers and ice sheets reached their maximum extent, covering a significant portion of the Earth's surface. They occurred during the Later Pleistocene, between 26,500 and 19,000 years ago, in which cold and dry climate significantly impacted plant and animal life, leading to the extinction of some species and the adaptation and survival of others (Li et al. 2020; Zhang et al. 2022). It was in the ice age (Clark et al. 2009), covering vast land, causing remarkable vegetation disappearance, and expanding deserts (Hou et al. 2018). 3) The recent profiles in the Holocene, from 1970 to 2000. 4) Future distribution scenarios in the 2050s.

Modeling framework and evaluation

To ensure the accuracy of sample points and avoid oversampling or biased sampling, we used the "Spatially Rarefy Occurrence Data for SDMs" tool to choose the locations (Fourcade et al. 2014; Brown et al. 2017). Eighty-three fossil sites and 116 recent macaque distribution locations were selected for this study (Fig. S1).

A procedure selecting the variables that are independent but closely related was completed by Principal Component Analysis (PCA), referring to the scores on the first three axes accounting for a significant part of the eigenvalue. The Kaiser-Meyer-Olkin (KMO) and Bartlett's tests were applied to define whether a variable is suitable for PCA (Toll and Van Luit 2013). The modeling was performed after the variables with low scores, among the highly correlated variables, had been removed based on the axes with higher loading values.

Two different models corresponding to variable types (BC, LU, and HP – Table 1) were established to conceive monkeys' suitable habitat distribution, referring to alternative climatic and environmental exponents and human population size – which have shaped and would drive their geographic distribution trajectories in the years to come.

BC models include a) retrospectively reconstructing suitable habitat areas for LIG and LGM periods separately; BC- LU- HP models include b) the suitable habitat distribution scenario between 1970 and 2000; and c) the future suitable habitat distribution scenarios in the 2050s.

Five models for four periods were analyzed with MaxEnt, with two main modifiable parameters - the Feature Class (FC) and the Regularization Multiplier (RM) - which can increase or decrease the model's fit. Since the default combinations of these two parameters cause overfitting (Porfirio et al. 2014; Qiao et al. 2015), we used the R package ENMeval (Muscarella et al. 2014) to select an optimal combination of FC and RM. They were repeated ten times in generating operating characteristic (ROC) curves of the models and obtaining the mean area under the curve (AUC). They are then used to assess model accuracy according to AUC values ranging from 0 to 1. A value of 0.5 represents a random model (Myerson et al. 2001). The point on the ROC curve, the tangent slope, equals 1, corresponding to the maximized sum of sensitivity and specificity (maxSSS) (Cantor et al. 1999). Compared with other methods, maxSSS, used as the threshold, has higher sensitivity and credibility (Liu et al. 2016). Thus, we applied a threshold at which the habitat is considered suitable, using the average of maxSSS for each model. Then, we use the natural breaks (Jenks) method to classify suitable regions into three grades – high, moderate, and low suitable areas (Calka 2018).

We also used the percentage of contribution and permutation importance to search for the dominant drivers influencing macaques' distribution (Phillips et al. 2006; Zhang et al. 2019a).

The five geo-ecological regions in China are the Northwest, Southwest, Central, Coastal, and Northeast (Huang et al. 2021; Zhang et al. 2022).

Distributional shifts

The centroids, the centers of suitable habitat distribution (Brown 2014), were compared for the LIG, LGM, and present and future (the 2050s). As for the expectation of prospective habitat distribution in the 2050s, we focus only on highly suitable areas.

Conservation and protected areas

It is necessary to oversee how macaques' distribution areas overlap with the protected areas (PAs) in China, a parameter assessing monkeys' conservation status. We downloaded PA data recorded in 2021 from the National Specimen Information Infrastructure (NSII, http://www.nsii.org.cn/2017/home.php), based on which we constructed the potential habitat corridors that macaques could use.

RESULTS

Established models

For LIG, PCA results show a 0.6 KMO value, and the second axis expresses the most significant AUC value (AUC = 0.98) among the three axes, accounting for 24.2% of the total variance, on which seven BC variables were selected (Table 1, Figs. S2 and S3). As for 1970–2000, the first PCA axis accounts for 39.7% of the total variance with a 0.6 KMO value and a 0.99 AUC value (Figs. S2 and S3), and five BC variables were chosen (Table 1). The optimal combination of feature class (FC) and regularization multiplier (RM) for all five models is presented in table S1.

Model accuracy was assessed by 10-fold cross-validation; all models' mean AUC_{TEST} values are greater than required for a significant threshold (0.5) (Fig. S4), implying the demonstrated predictions are excellent.

Variable contributions to MaxEnt prediction models are illustrated in figure S5. Regarding 1970-2000, var8 (33.5%), var16 (25.1%), and var5 (19.1%) play major roles, accounting for 77.7% of the total contribution. As for SSP2, var8 (42.3%), var5 (21.3%), and var16 (15.9%) are highlighted, making 79.5% of the total contribution. Concerning SSP5, 47.3% for var8, 21.9% for var5, and 14.2% for var16 are highlighted for their 83.4% of the total contribution.

Reconstructed habitat distribution

Macaques' diversity distribution profiles in the Pleistocene (LIG and LGM) are reconstructed based on fossil data and BC variables (Fig. 2). Regarding LIG, monkeys' highly suitable distribution areas were primarily concentrated in the east of the Southwest, south of Central, and Coastal regions. Moderately suitable areas were primarily in the south of the Southwest. Poorly suitable areas were principally

Table 1. BC, LU and HP variables selected for this study

Type	Code	Variables	Units
BC	var1	Mean diurnal range[1,2]	°C
	var2	The maximum temperature of the warmest month[1]	°C
	var3	The minimum temperature of the coldest month[1]	°C
	var4	Mean temperature of the wettest quarter[1]	°C
	var5	Mean temperature of driest quarter[2]	°C
	var6	Precipitation of the wettest month[1,2]	mm
	var7	Precipitation of the driest month[1,2]	mm
	var8	Precipitation of the warmest quarter[1,2]	mm
LU	var9	Forested primary land[2]	%
	var10	Non-forested primary land[2]	%
	var11	Potentially forested secondary land[2]	%
	var12	Potentially non-forested secondary land[2]	%
	var13	Rangeland[2]	%
	var14	Urban land[2]	%
	var15	Secondary mean biomass density[2]	kg C/m^2
HP	var16	Human population density[2]	number of people/km^2

Note: var1 to 8 are BC variables; var9 to 15 represent LU variables; and var16 is HP variable. [1]: the variables used in models for LIG and LGM periods; and [2]: the variables utilized for the models for 1970–2000 and the 2050s.

clustered in the north of the Central and south of the Northeast (Fig. 2a).

As for LGM, compared with LIG, highly suitable areas in the south of the Central and Coastal regions were degraded to moderately suitable ones, which shifted to the Central (Henan) and the Northwest (Shannxi). Poorly suitable areas in the Northeast shifted to the north Central region (Fig. 2b).

Modeled suitable habitat areas

Regarding suitable distributions based on BC- LU-HP variables, the current period (1970–2000) and future (the 2050s) were developed based on two different CO_2 emission scenarios, SSP2 and SSP5 (Fig. 3).

For 1970–2000 (Fig. 3a), highly suitable areas were concentrated in the eastern part of the Northwest (Shannxi) and southern Coastal regions. Moderately suitable areas are severely fragmented, mainly in the south of the Southwest (Guangxi) and Coastal regions (Guangdong), and the poorly suitable areas are primarily in the Central and northern Coastal areas.

Concerning the 2050s based on SSP2 (Fig. 3b), and compared to figure 3a, some highly suitable areas appearing in 1970–2000 would be expanded; some places would be transferred to moderately suitable regions, primarily in the Southwest, southeast of the Northwest, and the south of the Coastal areas. Referring to SSP5 (Fig. 3c) and compared with figure 3a, the highly suitable areas in the south of the Coastal and the Northeast of the Southwest would be downgraded to moderately suitable areas. In contrast, poorly suitable areas in the Northeast would be expanded.

Changes in distribution size and trajectories of the four spatial-temporal periods (LIG, LGM, 1970–2000, and 2050s) are illustrated in figure 4. Strikingly, the highly and moderately suitable habitats gradually decreased from LIG to SSP5. The total suitable area from LIG to LGM was reduced by 96,913 km^2. While SSP2 is considered, the total suitable area from the current to the 2050s would be expanded by 89,810 km^2, increasing by 2.53%. While SSP5 is referred to, the

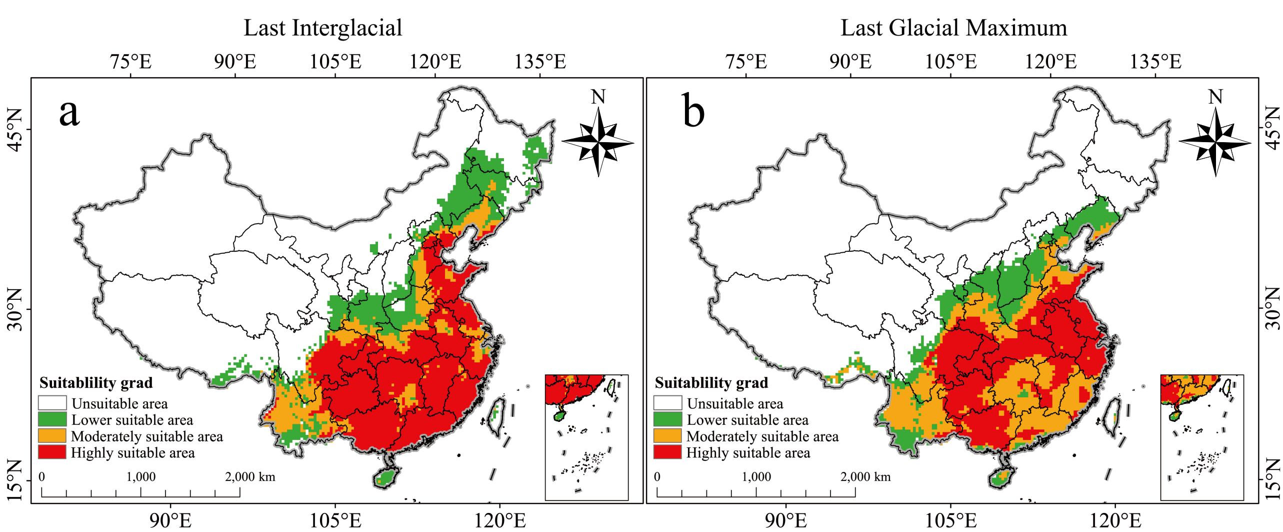

Fig. 2. Distribution of suitable habitat reconstructed with MaxEnt, a: LIG, and b: LGM.

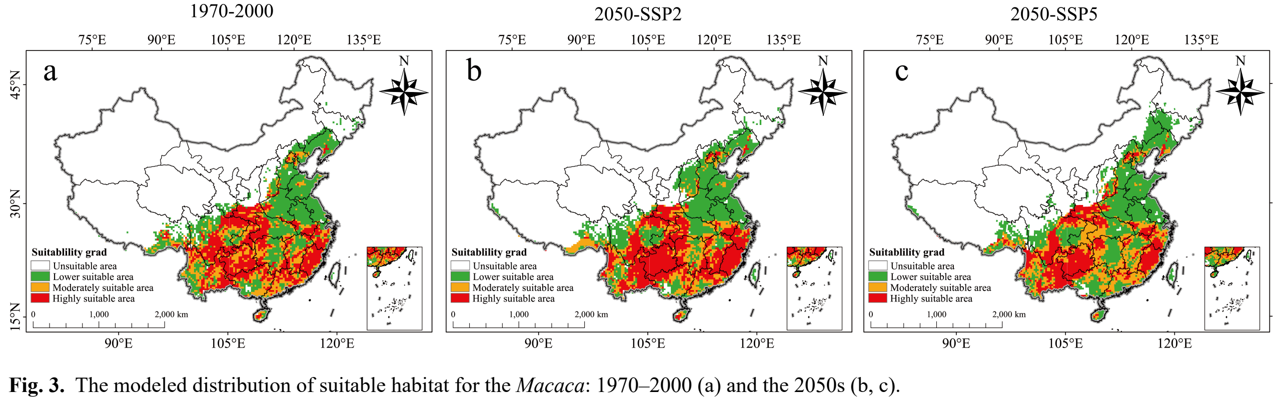

Fig. 3. The modeled distribution of suitable habitat for the *Macaca*: 1970–2000 (a) and the 2050s (b, c).

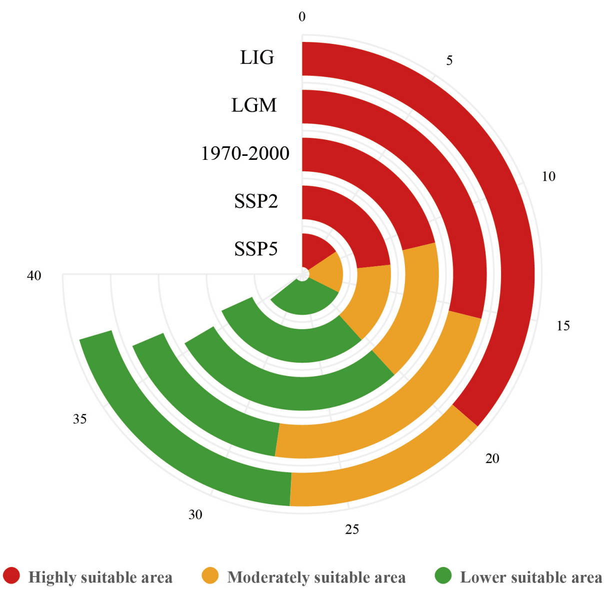

Fig. 4. Periodical suitable habitat changes of the macaques from LIG to the 2050s.

suitable distributions would decrease by 119,041 km^2, with a reduction of 3.35%.

Centroid shifts of the suitable distribution

Distribution centroid shifts of the suitable areas from LIG to 2050s are presented in figure 5. The distribution center of macaques during the LIG was located in Xuancheng City (31°45'27"N, 112°13'2") in Hubei, with an elevation of 56 m. Under the LGM, the center of suitable habitats would move southeast to Changyang Tujia Autonomous County (30°23'48"N, 110°48'44"E), with an elevation of 337 m, a total migration displacement of 202.2 km.

The centroid of 1970–2000 is in Wufeng Tujia Autonomous County, Hubei (30°16'7"N, 110°21'59"E), with an elevation of 1,749 m. Under SSP2, it would shift 21.1 km to Badong County (30°27'6.5880"N, 110°18'52"E) in the same province, with an elevation of 623 m. If SSP5 is considered, the centroid would move 65.2 km Northeast in Digui County (30°44'5"N, 110°46'34"E), with an elevation of 733 m.

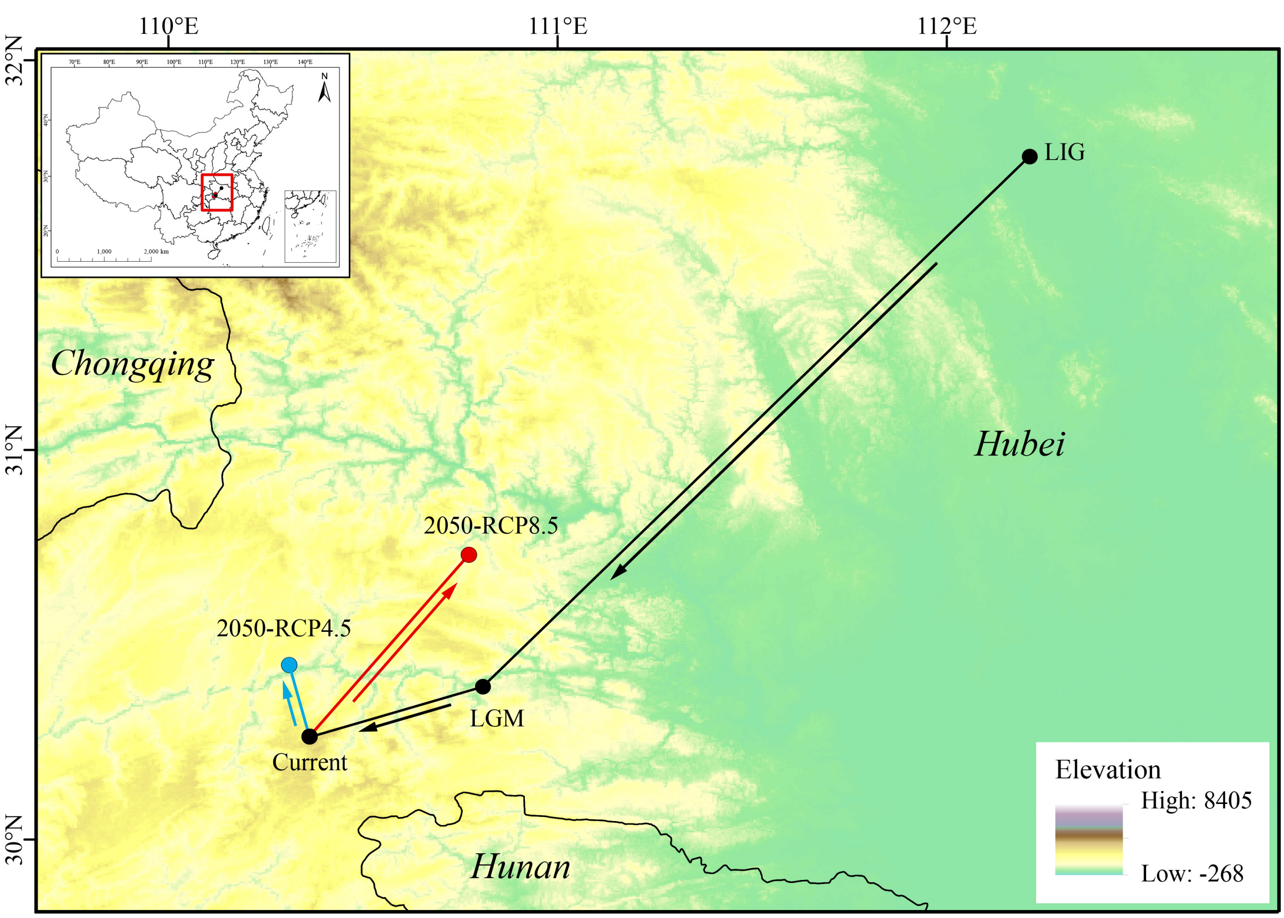

Fig. 5. The proposed centroid shift of suitable habitat of the macaques from LIG to the 2050s while the two emission scenarios are considered.

The relationship with PAs

Overlapping profiles between macaques' geographic distribution and the existing PAs are listed in table S2. Their 94.00% distribution in 1970–2000 and the 2050s (SSP2 and SSP5) is not and would not not be covered by current PAs. Further, we established the potential passing corridors for macaques in different periods based on the highly suitable habitat areas and PAs' resistance layers (Fig. 6). As to the period of 1970–2000, macaques should have 164 passages in highly suitable habitats, principally in Central and Southwest regions (Fig. 6a). As for SSP2 in the 2050s (Fig. 6b), compared with figure 6a, corridor numbers (115) would decrease significantly so in the southern Central and Southwest regions. Referring to SSP5 in the 2050s (Fig. 6c) and compared with figure 5a, corridors would decrease in the northern Central region, but increase in the southern Central. However, corridor lengths would become shorter following more fragmented habitats. As a result, the period's corridor number would be 182.

DISCUSSION

This study, as expected, provides scientific evidence and information to identify bioclimate, land use, and human-induced activity (population density) variables that have significantly shaped and would drive macaques' diversity and geographic distribution trajectories to the 2050s. The results provide scientific guidelines to amend the existing conservation strategies and management for macaques in the years to come, referring to their future shifting directions and survival

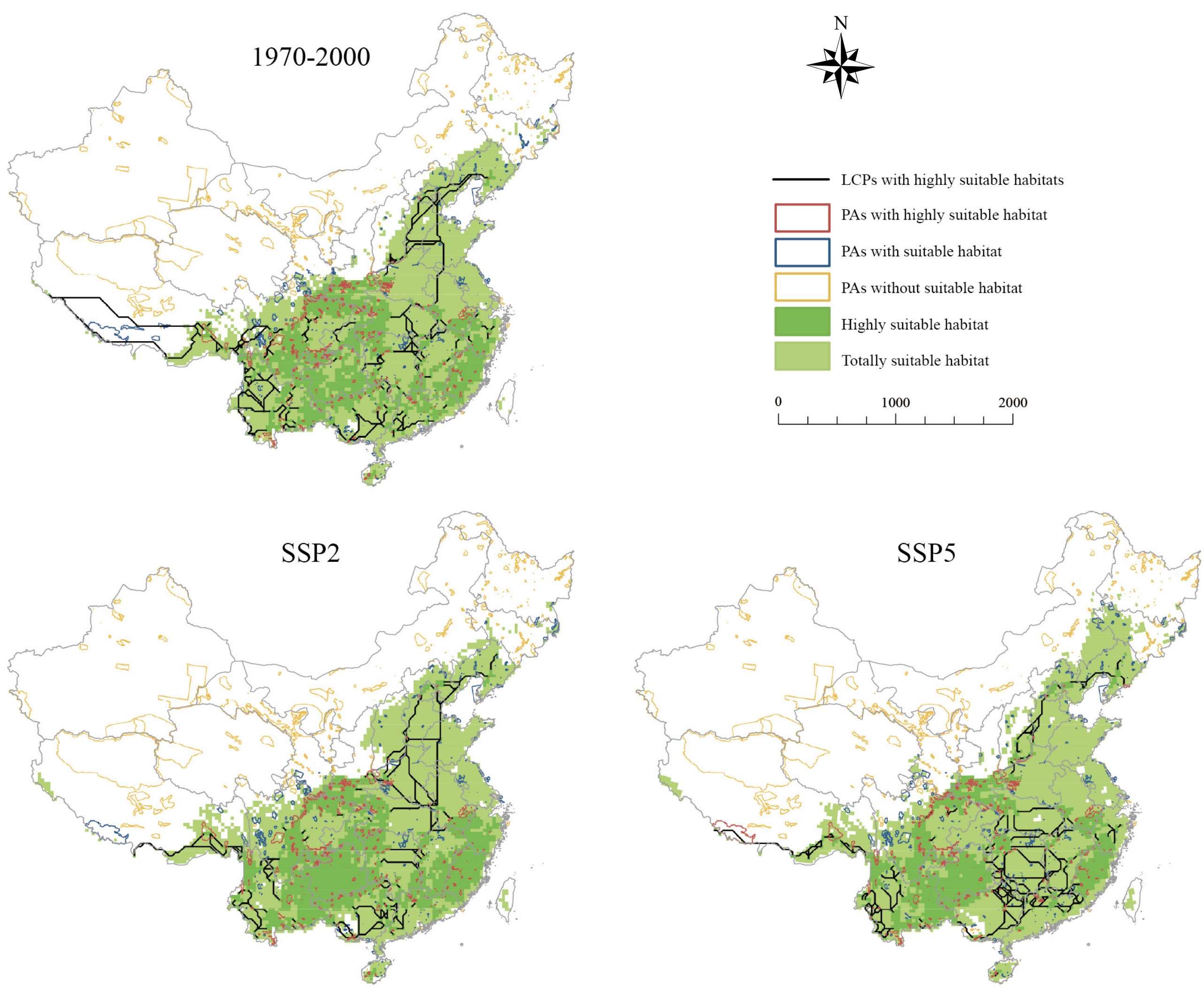

Fig. 6. Protection areas (PAs) overlap with highly suitable areas of the macaques, referring to different historical periods. The least-cost pathways (LCPs) migration corridors are proposed in highly suitable areas.

prospects in China, which will be shaped by the two greenhouse emissions scenarios (SSP2 and SSP5).

The variables selected for the MaxEnt model

Table 1 shows seven environmental and human population densities and eight bioclimatic variables selected to establish MaxEnt models to describe macaques' evolutionary changes and future distribution profiles. Three of them, the precipitation of the warmest quarter (var8), the mean temperature of the driest quarter (var5), and the human population density (var16), are those playing a decisive role in setting up the models for the current (1970–2000) and future (the 2050s) distribution profiles (Fig. S5).

Maintaining water balance is crucial for animals' survival, which can constrain their geographical environment and habitat selections (McCluney and Sabo 2009); one of the main reasons causing many mammal species to become extinct during the drought in the Later Pleistocene and the early Holocene (Jukar et al. 2021). This has occurred in some macaque species, such as *Macaca sylvanus* in Norfolk (Elton and O'Regan 2014) and Greece (Konidaris et al. 2022), *Macaca majori* in Italy (Zoboli et al. 2016), and *Macaca* cf. *M cyclopis* and *Macaca anderssoni* in China (Chang et al. 2012; Ito et al. 2014).

The extant macaque taxa now primarily reside in tropic-subtropic and temperate regions in North Africa and Asia (Galán-Acedo et al. 2019), and are less tolerant of droughty climates (Fleagle and Gilbert 2006). A positive relationship between habitat suitability and precipitation for *Macaca* (Fig. S6a) is like what was described in primate species in Southeast Asia (Wang et al. 2013); less precipitation would limit their access to food sources due to poor leaf and fruit production (Rosenzweig 1968; Wang'ondu et al. 2013). This study implies that climatic conditions or fluctuation would continue to be essential in driving macaques' diversity and distribution.

Unsurprisingly, the human population density variable is the primary driving force shaping macaques' future conservation by reducing habitat suitability (Fig. S6b). Intensified anthropogenic activities have also followed human population growth, leading to significant increases in cropland, pasture, and rangeland since the 1950s in China – the human population size increased from 540 million in 1949 to 1.4 billion in 2020 (Jo Huth 1990); cropland increased by 2549.2 × 10^4 hm^2 from 1949 to 2003, increasing 47.2 × 10^4 hm^2/year (Bi and Zheng 2000; Feng et al. 2005). Pastures and croplands have separated suitable distributions and migration paths, which have blocked genetic exchanges and caused population reduction and extinction (Forman and Alexander 1998; Saxena et al. 2020). Such a scenario applies explicitly to some macaque populations in Shanxi (Zhou 2014).

Distribution changes

According to figure 2, the reconstructed suitable distributions for LIG and LGM indicate that macaques were principally concentrated in the eastern Southwest, Central, and Coastal regions. Such a distribution pattern corresponded to the dispersal and radiation scenarios of the monkeys during the Pliocene and Pleistocene (Li et al. 2020; He et al. 2022; Zhang et al. 2022): Asian macaques migrating from North Africa entered a Convergence-Divergence Center in Southwest China through Europe and Western Asia as illustrated in figure 1. They then continued the dispersion and radiation along the three major rivers in the East Asian continent (Yangtze, Yellow, and Pearl), reaching far east Asia (Taiwan, Korea, and Japan). Others spread to Southeast Asia, occupying Borneo, Malaysia, and Indonesia (Li et al. 2020). However, as found in this study, most taxa remain in Southwest China (Fig. S1), where they initiated dispersion and radiation in East and Southeast Asia (He et al. 2022; Zhang et al. 2022), implying that the Southwest is still their central distribution region.

Compared to the LIG (Fig. 2a), some highly suitable areas during the LGM were degraded, especially in Northern China, the Sichuan Basin, and the Qinling-Daba Mountain (Fig. 2b). This change must have been associated with the severe monsoon generating the cold and dry climate during the Quaternary (Zhang 2004), following the rapid uplift of the Himalayan orogeny and the Qinghai-Tibet Plateau. As a result, some animals, including primates, survived in regions with relatively stable environments and ecological niches during the Later Pleistocene (Jablonski 1993). Macaques (*Macaca*) reached Northern China, the northern limit of the subtropic zone, during the Early or Middle Pleistocene (Zhang 2002). The distribution extended northwards to the Liaodong Peninsula, northeast Beijing, and the northernmost Jinniushan (Jablonski 1993). Tropical and subtropical forests migrated southward from north to south China (Huang et al. 2021), so macaques and other primate species were pushed southwards (Jablonski 1998; Zhang et al. 2022).

Compared to LGM (Fig. 2b), the size and regions of the current suitable macaque distributions have decreased (Figs. 3 and 4), so that they were prominently located in high mountainous areas in the Yunnan-Guizhou Plateau in the Southwest, as well as alongside the Qinling Mountains in southeastern Northwest, and southern Coastal and Central regions (Zhejiang-Fujian). Such modified profiles, as mentioned above, must have been caused by accelerated human-induced activities in China during the Holocene, such as extensive deforestation and cultivation of the lowlands (Olson and James 1982; Ma et al. 2020), which was accelerated following further land exploitation and indiscriminate deforestation, particularly after the Qin and Han Dynasties (Ramankutty and Foley 1999). After 1,700 BP, 5 million m^2 of natural vegetation had been converted into agricultural land and pasture (Pongratz et al. 2008). Further, the two opium wars (1800–1849 and 1850–1899), the Second World War (1939–1945), the Civil War (1900–1949), and the post-war period (1950 ~) aimed at increasing agricultural demands for the rapidly increasing human population, have caused a series of waves of significant destruction to natural environments and devastation to animal distributions (Pan et al. 2016; Huang et al. 2021). Over the last 40 years, the unprecedented socioeconomic development has led to significantly increasing road construction, cropland, and pasture – which, as indicated in the study, will further push the monkeys and other animals to higher mountains.

Prospective conservation

The two profiles of the suitable distribution for the macaques in the 2050s, proposed with SSP2 and SSP5 emission scenarios, and presented in figures 3 and 4, demonstrate that macaques would be distributed in the southern and eastern Southwest, southeastern Northwest, and southeastern Coastal regions. Compared to the current profiles, the highly suitable distribution would be slightly increased referring to SSP2 but continue reducing considering SSP5 (Fig. 4), implying that the greenhouse emission patterns will play a significant role in shaping macaques' future distribution and conservation.

The trend of moving to lower elevations in some areas in the following years (Fig. 5) could be closely related to what has been done by the Chinese Government over the last two decades after realizing the seriousness and urgency of conservation and environmental protection, such as implementing the six Key Forestry Projects (SKFPs), targeting 76 million ha of land for afforestation and reforestation, covering 97% of China's counties (Wang et al. 2007). As a result, total forest coverage in China increased from 16.55% in the 1990s to 22.9% in 2018 (Song and Zhang 2010; Cui and Liu 2020). Most significantly, logging natural forests for commercial purposes has been banned in some places bearing remarkable diversity of hot spots, such as the upper reaches of the Yangtze River and the upper and middle reaches of the Yellow River, involving 13 provinces (Xu et al. 2006). On the other hand, PAs have gained substantial attention; as of 2018, 11,800 PAs have been established in China, covering about 18% of China's terrestrial area and 4.1% of its marine area (Feng et al. 2021).

Unfortunately, referring to table S2, macaques are left out of such PA promotion: more than 94.0% of their suitable habitats from now on to the 2050s are not covered by PAs, indicating their conservation prospect is challenging. Implementing this study's proposed conservation strategies (outlined below) is urgent.

On the other hand, migration corridors for the macaques would be noticeably reduced, referring to SSP2, corresponding to further fragmented habitats. Such corridors would be more condensed in the southern Central, featured by shorter and isolated, considering SSP5 (Fig. 6), indicating that their expected migration space would be further confined. This phenomenon especially applies to some threatened taxa, such as the Arunachal macaque, distributed only in southeastern Tibet (Kumar et al. 2020), which is at the edge of extinction due to hunting and retaliatory killing in response to crop damage (Sinha et al. 2006). The other species with reduced habitats and moving corridors are the northern pig-tailed macaques restricted to southwestern Yunnan, west of the Yuanjiang River and east of the Nujiang River (Sun et al. 2020), and the white-cheeked macaques, newly discovered in southeastern Tibet (Li et al. 2015).

According to figure 6, more potential habitat corridors for macaques are currently distributed in the Southwest and Central regions, with poor connectivity in the southern Central region, following highly suitable habitats being fragmented in the 2050s, referring to SSP5 (Fig. 6c). Besides macaques, other wildlife would suffer in this area, *e.g.*, the Chinese giant salamanders (*Andrias davidianus*) (Zhang et al. 2020), and black-faced spoonbill (*Platalea minor*) (Hu et al. 2010).

The proposed macaque distribution trajectories assume that the seven species' conservation situations are equally weighted. However, there is significant variation among species regarding their differences in ecology, environment, geographic contour, elevation, and human activities. In general, the following three groups should be considered differently:

a) *Macaca mulatta* is characterized by stable population size and broad distribution. Its main threat is conflicts with humans for cropland feeding (Lu et al. 2018; Wu and Long 2020).

b) *Macaca arctoides*, *M. thibetana* and *M. assamensis*. They primarily face the pressures of habitat fragmentation and degradation caused by expanded urbanization, rising human activity, and global climate change (Li 1999; Boonratana et al. 2020).

c) *Macaca leucogenys*, *M. munzala* and *M.*

leonina. Besides narrow distribution and small population sizes, their biological and distribution issues are less understood. The main threats are hunting, land conversion, hydroelectric power station construction, and habitat fragmentation (Ma and Wang 1988; Sinha et al. 2006; Li et al. 2015).

CONCLUSIONS

With the datasets of fossils and extant taxa of the macaques, this study integrally analyses the variables associated with bioclimatic components, environmental characters, and human population – which have significantly shaped macaques' evolutionary distribution patterns from LIG to the present, based on which their future distribution profiles in the 2050s are constructed, referring to the two CO_2 emission scenarios. Some main results include:

1). Monkeys' suitable distributions, initially concentrated in the Southwest, Central, and Coastal regions during LIG and LGM, started reducing in the eastern Southwest and the south of Central and Coastal after LGM.

2). Diminishing carbon emissions due to deforestation, coal combustion, and other human activities but increasing habitat restoration, which China has emphasized, would undoubtedly allow the macaques to maintain their current distribution areas.

3). Precipitation fluctuation, the increased human population size, and temperature changes would continue to play a dominant role in the potential development of suitable distributions for the macaques.

4). To allow the macaques and the other animals to maintain sustainable diversity and more suitable distributions for conservation purposes, we propose a) restoring some fragmented forests in suitable distribution areas; b) expanding the sizes of established protected areas or increasing buffer zones with ecological corridors between the fragmentations by roads and human construction.

5) The Southwest and southeast of the Northwest region in China will provide valuable future shelters for the monkeys and perhaps other animals, considering more migration corridors will be reserved there. Thus, those areas should be prioritized in their conservation.

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Availability of data and materials: The datasets supporting this article have been uploaded as part of the supplementary material. Climatic variables were obtained from the WorldClim bioclimatic dataset version 1.4 and 2.1 (https://www.worldclim.com/) (https://www.worldclim.org/) and the Land use variables were from Land-use Harmonization (https://luh.umd.edu/data.shtml). Human Population variables were downloaded from Spatial Population Scenarios (www.cgd.ucar.edu/iam/modeling/spatial-population-scenarios.html).

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Supplementary materials

Fig. S1. Macaques' fossil locations in the Pleistocene and extant distribution profiles of 1970–2000. (download)

Fig. S2. Heatmap for correlation analysis of *Bioclimatic variables* (BC) Note: a: LIG period; b: 1970–2000 period. bio2: mean diurnal range; bio5: the maximum temperature of the warmest month; bio6: the minimum temperature of the coldest month; bio8: mean temperature of the wettest quarter; bio9: mean temperature of the driest quarter. bio13-bio19 related to the precipitation: bio13: the wettest month; bio14: the driest month; bio18: the warmest quarter; and bio19: the coldest quarter. (download)

Fig. S3. Principal component analysis for BC variables in LIG and 1970–2000. (download)

Fig. S4. Precision evaluation of MaxEnt model for the five periods. Model accuracy was assessed by 10-fold cross-validation. All models' mean AUCTEST values are greater than required for a significant threshold of the random prediction (0.5), implying the modeled predictions are "excellent." As for LIG and LGM, the mean AUCTEST is 0.983 ± 0.010 and 0.982 ± 0.006, respectively. The same values are 0.989 ± 0.002 for 1970–2000; 0.988 ± 0.002 for SSP2; and 0.988 ± 0.004 for SSP5. (download)

Fig. S5. Percentage contribution of the variables used for MaxEnt prediction models. (download)

Fig. S6. Response curve of the precipitation of the warmest quarter (var8) and the human population density (var16). (download)

Table S1. BC, LU and HP variables selected for this study. (download)

Table S2. The optimized parameters of MaxEnt models generated by ENMeval*. (download)

Table S3. Overlapping area (km^2) and proportion (%) both core areas (highly suitable areas) and total suitable areas against protected areas (PAs). (download)