Evolutionary Geographic Changes of the Macaques in Mainland East Asia during the Quaternary and Their Prospective Conservation

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[1]Northwest University

June 6, 2023

Abstract

Understanding how ecological and environmental changes, anthropogenic activities, and climate have driven and will direct animals' development and predicting their prospective distribution profiles in the Quaternary are essential to making a tangible conservation strategy. Macaques (*Macaca*) distributed in mainland East Asia provide an ideal research model for such an effort. We reconstruct macaques' geographic distribution profiles during the Quaternary, 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 perspective distribution in the 2050s. The results show their suitable habitats during LIG and LGM were mainly in Southwest, Central, and Coastal China. A noticeable distribution reduction started in LIG and persisted until the current (1970-2000). Their distribution centroid would shift northward to mountainous regions, mainly in Southwest China, where more migration corridors would be reserved for their future development. Also, the results indicate that China's Protected Area currently does not cover more than 87% of macaques' habitats, 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 in Quaternary.

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[a] Shaanxi Key Laboratory for Animal Conservation, College of Life Sciences, Northwest University, Xi'an 710069, China.

[b] International Centre of Biodiversity and Primate Conservation Centre, Dali University, Dali, China.

[c] School of Human Sciences, The University of Western Australia, Perth, WA 6009

# These authors contributed equally to this work.

*Corresponding authors.

E-mail addresses: baoguoli@nwu.edu.cn (B.G. Li), ruliang.pan@uwa.edu.au(R.L. Pan)

Abstract :

Understanding how ecological and environmental changes, anthropogenic activities, and climate have driven and will direct animals' development and predicting their prospective distribution profiles in the Quaternary are essential to making a tangible conservation strategy. Macaques (*Macaca*) distributed in mainland East Asia provide an ideal research model for such an effort. We reconstruct macaques' geographic distribution profiles during the Quaternary, 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 perspective distribution in the 2050s. The results show their suitable habitats during LIG and LGM were mainly in Southwest, Central, and Coastal China. A noticeable distribution reduction started in LIG and persisted until the current (1970-2000). Their distribution centroid would shift northward to mountainous regions, mainly in Southwest China, where more migration corridors would be reserved for their future development. Also, the results indicate that China's Protected Area currently does not cover more than 87% of macaques' habitats, 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 in Quaternary.

Keywords: Climate and environmental Changes in Quaternary; Conservation strategy; Human-induced activities; Macaques' evolutionary geographic distribution; MaxEnt model; Mainland East Asia.

1. Introduction

Over the years, global ecological changes and environmental devastation triggered by human-induced activities and climate alteration have increased globally (Ofori et al., 2017; Measey et al., 2019). We are now facing enormous pressures that are 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 in the Quaternary (Chen et al., 2011; Hoffmann and Sgrò, 2011), resulting in more than 75% alteration in contemporary terrestrial ecosystems (Venter et al., 2016), following extensive agricultural changes and deforestation (Gries et al., 2019), and accelerated expansion of urbanization (Eötvös et al., 2018; Duncan et al., 2020).

Thus, ecological changes and human-induced activities during the Quaternary, which have remarkably caused climate changes and faunal and floral geographic alterations, have created unprecedented biodiversity diminishing 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 that cannot respond rapidly are pushed to extinction (Radchuk et al., 2019; Doherty et al., 2021). Such as, mountain lions (*Puma concolor*) exhibited significant antipredatory behavior changes in response to habitat alteration, resulting in a 34% reduction in their distribution (Suraci et al., 2019), forcing them to abandon high-risk home ranges (Schuette et al., 2013). Following global warming, glaciers, and sea ice melting rapidly, the population of polar bears (*Ursus maritimus*) at the southernmost end of the Arctic region has declined sharply (Derocher et al., 2004). 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 phenomenon especially applies to non-human primates, who are more sensitive to those changes and entirely dependent on forested ecosystems (Estrada et al., 2017; Zhang et al., 2019b). That is why over 60% of extant global species are on the edge of extinction (Estrada et al., 2017; Carvalho et al., 2019). Regarding the situation in mainland East Asia, such a scenario is even more gloomy – 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; Zhang et al., 2022): they originated in Africa and started the migration to Europe and Asia following the collision of the Afro-Arabian plate with Eurasia during the Oligocene-Miocene (23.8-18 Mya), which created a land connection between Arabia and Southwest Asia, making many animal taxa migrated from Africa, via Europe, to Asia since the Miocene (Roos and Zinner, 2015), including macaques. 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 finally settled down in Southwest China during the Pliocene. They continued distributing to East and South Asia through alternative dispersal paths during the Quaternary (Li et al., 2020; Zhang et al., 2022). Eight extant species are now distributed in mainland East Asia: rhesus macaques (*Macaca mulatta*), the northern pig-tailed macaque (*M. leonina*), the stump-tailed macaque (*M. arctoides*), Formosan rock macaque (*M. cyclopis*) in Taiwan, Assamese macaque(*M. assamensis*), the Tibetan macaque (*M .thibetana*), the Arunachal macaque (*M. munzala*), and the white-cheeked macaque (*M. leucogenys*). They are classified as Class II or I of Nationally Protected Wildlife in China and are included on the IUCN Red List of threatened species (IUCN, 2022). Over the past two millennia, global climate change and human activities (including dramatic population explosion and resource depletion, agricultural expansion, overexploitation, etc.) have led to severe fragmentation of suitable habitats and gradual habitat degradation of suitable habitats for macaque species, resulting in a progressive decline in population size (Li et al., 2015; Zhao et al., 2021). Although some macaque species have experienced population growth due to effective conservation measures, others are still on the verge of extinction, with meager numbers of individuals in the wild and a lack of systematic and comprehensive data on their status and distribution. Thus, the conservation of macaques in China faces a significant challenge (Li et al., 2020; Huang et al., 2021). It is necessary to perform further studies on these species to provide scientific and practical conservation measures referring to their geographical changes during the Quaternary.

Species Distribution Models (SDMs) are statistical tools based on environmental and species distribution data to estimate species preferences for habitat, which are widely used to explore the trajectories of geographic changes (Guisan et al., 2013). 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). However, using only current occurrence data to train SDM may reflect incomplete species ecological niches that cannot match past climatic environments, likely offering limited information to dynamically identify the drivers of their early declines leading to their current reduced population status (Scheele et al., 2017). Paleontological fossils provide unique perspectives for exploring the past existence of species in time and space (Lentini et al., 2018). Until now, relatively few studies have combined fossil data with SDM to provide a longer time-scale perspective for geographic changes and management of threatened animals due to difficulties in data collection and quantification of long-time-scale ecology (Nogues-Bravo et al., 2016; Gibson et al., 2019). Establishing dynamic spatial-temporal distribution models, referring to the alterations of climate, vegetation types, geological features, anthropogenic activities, and evolutionary changes, is demanded to make a tangible conservation strategy, especially in expecting their shifting direction and survival prospects. Such a model allows us to identify appropriate possible geographic changes, which can be referred to conservation measurements in advance. Macaque (*Macaca)* in mainland East Asia, including fossil and extant taxa, and their distribution profiles from the beginning of the Quaternary (Late Pleistocene) to the present can provide ideal materials for such an endeavor. Thus, this study's aims: 1) with the variables relevant to the changes in the environment, climate, ecology, geography, and human-induced activities to establish the models reconstructing macaques' past, current, and future distributions patterns of suitable habitats during the Quaternary; 2) identify the significant factors driving such changes; and 3) establish a database-driven geographic model for macaques.

2. Material and methods

2.1 Data of macaques and variables

The project includes datasets of geographic distributions of the fossil macaques found in the Pleistocene. They comprised *Macacayoungi* , *M. jiangchuanensis* , *M.anderssoni* , *M. mulatta* , *M. robustus* , and *M.* spp., and eight extant species in mainland China –*M. mulatta* , *M. arctoides* , *M. leonina* ,*M. assamensis* , *M . thibetana* , *M. munzala* and *M. leucogenys* , and another one in Taiwan Island (*M. cyclopis*). The database was collected from a broad literature review of academic journals, government annals, and archives, magazines, and books in Chinese (Please see the details in Supplementary information). Unfortunately, it is difficult, if not impossible, to define the relationship between fossils taxa and extant crown species – they are extensively overlapped in distribution, so all the taxa were analyzed at the genus (*Macaca*) other than the species level.

Nineteen variables are relevant to climatic, ecological, and environmental alterations, *Bioclimatic variables* (BC). They 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 primates (colobines and apes), macaques in East Asia started continental dispersion and radiation in the Late Miocene and Early Pliocene, about 5-6 Mya, from Western China. 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 Quaternary, the blooming period of the Asian macaques (Zhang et al., 2022), the fossil distribution of the macaques was analyzed also.

We used the *shared social-economic pathways* (SSPs) to analyze BC variables to predict the 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 greenhouse emission (GHG) 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 strategies 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.

2.2 Periodic distribution models

Four different evolutionary development distribution models were analyzed: **1**) the Last Interglacial Period (LIG, ˜140,000 – 120,000), featured by modern humans (*Homo sapiens*) starting the noticeable expansion and impacting environments (Hershkovitz et al., 2018; Harvati et al., 2019), progressively accelerated since then (Cavalli-Sforza et al., 1993);**2**) the Last Glacial Maximum period (LGM, 22,–00 - 19,000), the Late Pleistocene in which macaques reached their maximum booming on the continent (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; and **4**) future distribution scenarios in the 2050s.

2.3 Modeling framework and evaluation

To ensure the accuracy of sample points and avoid oversampled or biased sampling, we used "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 (Figure S1 in the Appendix).

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 on the axes with higher loading values.

Two different models corresponding to variable types (*BC* ,*LU* , and *HP* – Table S1 in Appendix) were established to conceive macaques' 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 habitats distribution scenarios in the 2050s.

Five models for four periods were analyzed with the MaxEnt model, 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 to generate the models' operating characteristic (ROC) curves and obtain 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 point where the habitat is considered suitable, using the average of maxSSS for each model. Then we use the natural breaks (Jenks) method to classify appropriate regions into three grades – high, moderate, and lower suitable areas (Calka, 2018).

We also used the contribution percentage to find the dominant drivers influencing macaques' distribution (Phillips et al., 2006; Zhang et al., 2019a).

As for the geo-ecological regions in mainland East Asia, five in number – Northwest, Southwest, Central, Coastal, and Northeast China (Huang et al., 2021; Zhang et al., 2022).

2.4 Distributional shifts

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

2.5 Protected areas

It is also necessary to oversee how macaques' distribution areas are overlapped with the protected areas (PAs) on the mainland, a parameter assessing macaques' conservation status. We downloaded 3,381 PAs data in 2021 from the *National Specimen Information Infrastructure*of *China* (NSII, http://www.nsii.org.cn/2017/home.php), processed missing and no vector extent data. A total of PAs with an area of about 1,079,934 km^2 were obtained, based on which we constructed the potential distribution of habitat corridors that macaques could use.

3. Results

3.1 Established models

As 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 S1, Figure. S2, and S3 in Appendix). 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 (Figure S2 and S3 in Appendix), and five *BC* variables were chosen (Table S1). The optimal combination of *feature class* (FC) and*regularization multiplier* (RM) for all five models is presented in Table S2.

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) (Figure S4 in the Appendix), 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 significant 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 contribution. Concerning SSP5, 47.3% for var8, 21.9% for var5, and 14.2% for var16 are stressed for their 83.4% of the total contribution.

3.2 Reconstructed geographical distribution

Macaques' diversity distribution profiles in the Pleistocene (LIG and LGM) are reconstructed based on fossil data and *BC* variables (Figure 1). Regarding LIG, macaques' highly suitable distribution areas were primarily concentrated east of the Southwest, south of Central, and Coastal. Moderately suitable areas were mainly in the south of the Southwest. Poorly suitable areas were principally clustered in the north of the Central and south of the Northeast (Figure 1A).

As for LGM, compared with LIG, highly suitable areas in the south of the Central and Coastal were degraded to moderately suitable ones, which shifted to the Central (Henan) and the Northwest (Shannxi). Poorly suitable areas in the Northeast, moving to the north of the Central (Figure 1B).

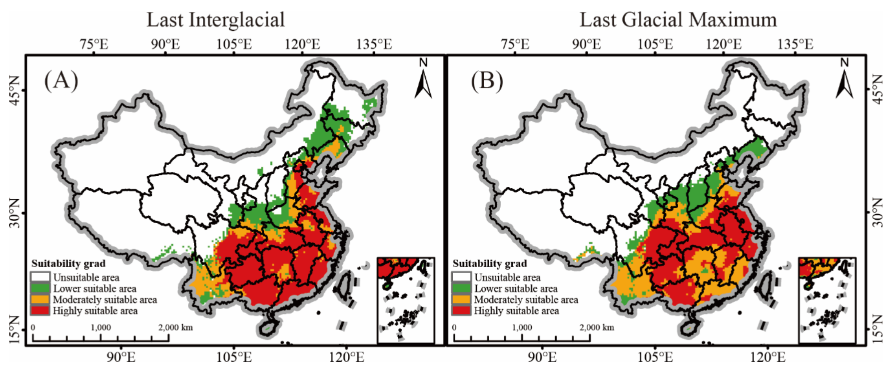

Figure 1 Distribution of suitable habitat reconstructed with MaxEnt, a: LIG, and b: LGM.

3.3 Modeled suitable distribution 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 (Figure 2).

As for 1970-2000 (Figure 2A), highly suitable areas concentrate in the eastern part of the Northwest (Shannxi) and south of Coastal. Moderately suitable areas are severely fragmented, mainly in the south of the Southwest (Guangxi) and Coastal (Guangdong), and the poorly suitable areas are primarily in the Central and northern Coastal.

Concerning the 2050s based on SSP2 (Figure 2B), and compared to Figure 2A, 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. Referring to SSP5 (Figure 2C) and compared with Figure 2A, the highly suitable areas in the south of the Coastal and the northeast of the Southwest would be downgraded to the moderately suitable area. In contrast, poorly suitable areas in the Northeast would be expanded.

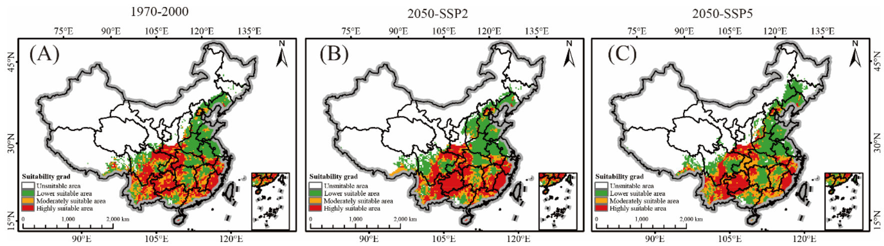

Figure 2 The modeled distribution of suitable habitat for the *Macaca* : 1970-2000 (A) and the 2050s (B, C)

Changes in distribution size and trajectories of the four spatial-temporal periods (LIG, LGM, 1970-2000, and 2050s) are illustrated in Figure 3. What strikingly changed is the highly and moderately suitable habitats that have gradually diminished 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 disappeared suitable distribution area would be 119,041 km^2, diminishing 3.35%.

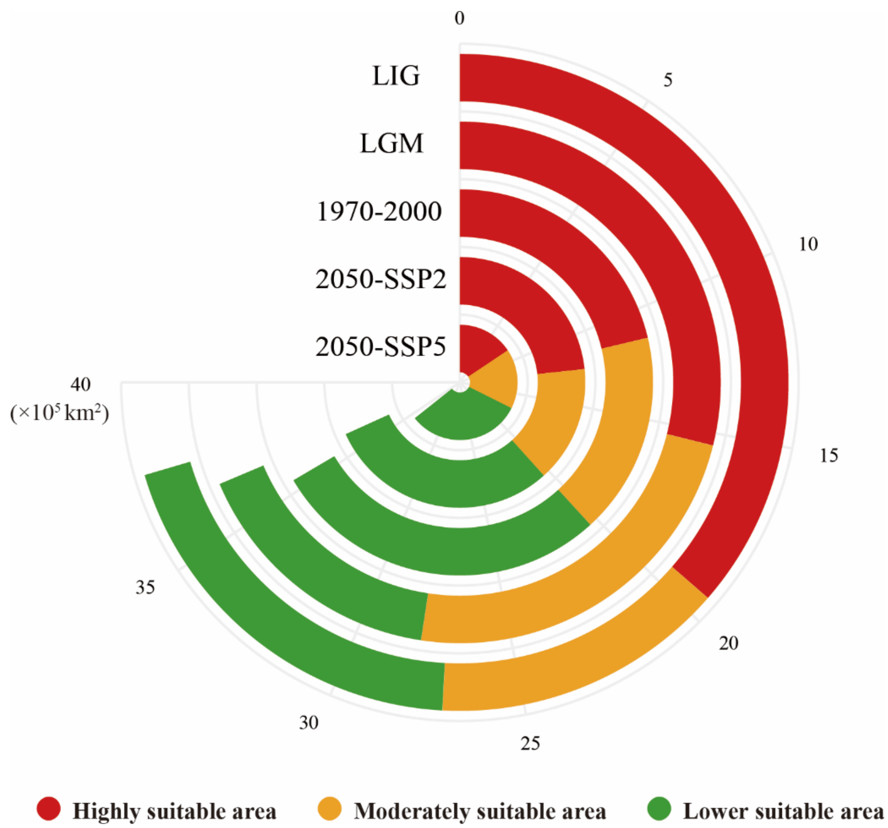

Figure 3 Periodical suitable habitat changes of the macaques from LIG to the 2050s

3.4 Centroid shifts of geographic distribution

Distribution centroid shifts of the suitable distribution area from LIG to 2050s are presented in Figure 4.

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, 110deg21'59" E), with an elevation of 1,749 m. While SSP2 is reckoned, it would shift 21.1 km to Badong County (30deg27'6.5880" N, 110deg18'52" E) in the same province, with an elevation of 623 m. If SSP5 is considered, the centroid will move 65.2 km northeast in Digui County (30deg44'5" N, 110deg46'34" E), with an elevation of 733 m.

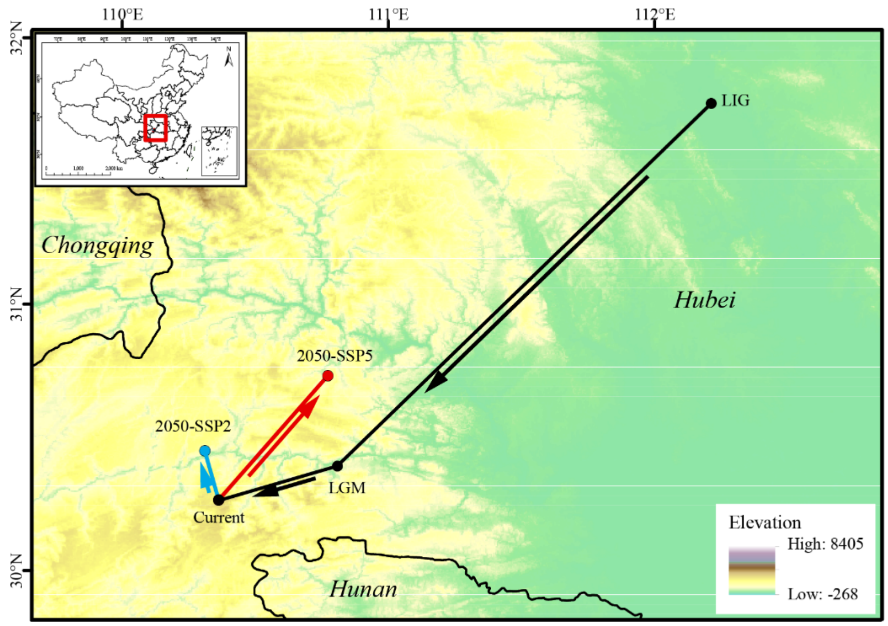

Figure 4 The proposed centroid shift of suitable habitat of the macaques from LIG to the 2050s while the two emission scenarios are considered

3.5 Geographical Changes and PAs

Overlapping profiles between macaques' geographic distribution and the existing PAs are listed in Table S3. Their 87% distribution in 1970-2000 and the 2050s (SSP2 and SSP5) are /would not be covered by current PAs. Further, based on the highly suitable habitat areas and PAs' resistance layers, we established the potential passing corridors for macaques in different periods (Figure 5). As for 1970-2000, macaques should have 164 passages in highly suitable habitats, principally in Central and Southwest (Figure 5A). As for SSP2 in the 2050s (Figure 5B), compared with Figure 5A, such corridor number (115) would decrease significantly in the southern Central and Southwest regions. Referring to SSP5 in the 2050s (Figure 5C) and compared with Figure 5A, that number in northern Central would decrease but increase in southern Central. However, corridor lengths would become shorter following more fragmented habitats. As a result, the period's corridor number would be 182.

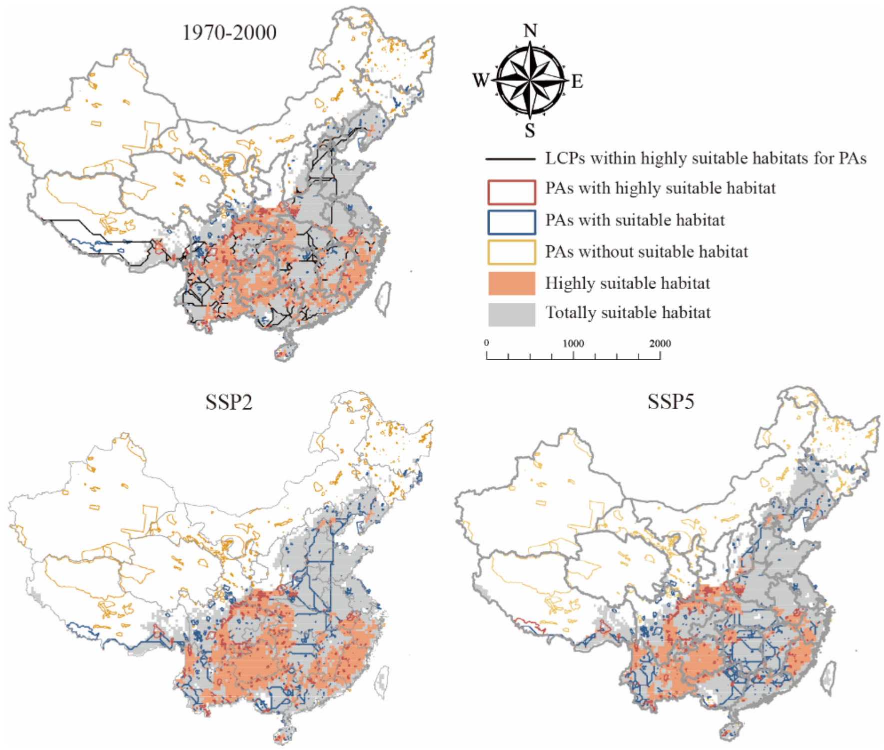

Figure 5 Overlapping of the protected areas (PAs) and highly suitable areas of the macaques in different periods. The least-cost pathways (LCPs) migration corridors are proposed in highly suitable areas

4. 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 from the Pleistocene to the 2050s of the Quaternary. In addition to demonstrating how macaques have been evolutionarily changed in geographic distribution during the epoch, the results also provide scientific guidelines to amend the existing conservation strategies and management for macaques in the years to come, referring to their future geographical shifting directions and survival prospects in mainland East Asia, which would be shaped by the two greenhouse emissions scenarios (SSP2 and SSP5).

4.1 The variables selected for the MaxEnt model

Table S1 shows seven environmental and human population densities and eight bioclimatic variables were selected to establish MaxEnt models describing 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 (Figure S5).

Rainfall and other water sources are crucial for animals' survival, which can constrain their geographical environment and habitat selections; such as, elephants' movement closely tracks precipitation-driven vegetation dynamics in a Kenyan forest-savanna landscape (Bohrer et al., 2014). One of the main reasons causing many mammal species to become extinct is the drought in the Later Pleistocene and the early Holocene (Jukar et al., 2021), such as that occurred in some macaque species, *Macaca sylvanus* in Norfolk (Elton and O'Regan, 2014) and Greece (Konidaris et al., 2022), *Macaca majori* in Italy (Zoboli et al., 2016),*Macaca* cf. *M. cyclopis* and *Macaca anderssoni* in China (Chang et al., 2012; Ito et al., 2014). Studies of climate impacts on the distribution of extant non-human primates have been few (Bernard and Marshall, 2020; Stewart et al., 2020); regarding that related to the taxa in China, it is reported that isothermality and temperature of the driest quarter are critically affecting the distribution of the gray-white snub-nosed monkey (*Rhinopithecus bieti*) – temperature might act as a reproductive regulator for the onset of estrus and mating season (Zhao et al., 2019).

The extant macaque taxa now primarily reside in tropic-subtropic and temperate regions in North Africa and Asia (Mittermeier et al., 2013; Galán-Acedo et al., 2019), less tolerating droughty climates (Fleagle and Gilbert, 2006). A positive relationship between habitat suitability and precipitation for *Macaca* (Figure S6) is like what was described in primate species in Southeast Asia (Wang et al., 2013); less rainfall 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 geographical changes by reducing habitat suitability (Figure S6). 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) in which, cropland increased by 2549.2×10^4 hm^2 from 1949 to 2003, increasing $47.2\times10^4 hm^2$/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).

4.2 Distribution changes

According to Figure 1, the reconstructed-suitable distributions for LIG and LGM show that macaques were principally concentrated in the eastern Southwest, Central, and Coastal. Such a distribution pattern corresponded to the dispersal and radiation scenarios of the macaques 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 aforementioned. 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 (Figure 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 (Figure 1A), some highly suitable areas during the LGM were degraded, especially in Northern China, the Sichuan Basin, and the Qinling-Daba Mountain (Figure 1B). 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 the 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). What followed up was that tropical and subtropical forests migrated southward from north to south China (Huang et al., 2021), so macaques and other primate species were pushed southern movement (Jablonski, 1998).

Compared to LGM (Figure 1B), the size and regions of suitable distributions of the current macaque distribution have reduced (Figure 2 and 3), 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 (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 exploiting lands and indiscriminate deforestation, particularly after the Qin and Han Dynasties (Ramankutty and Foley, 1999). So 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 increased human population, have caused a series of waves of significant destroying natural environments and devastating animal distributions (Pan et al., 2016; Huang et al., 2021). Over the last 40 years, the unprecedented social-economic development has led to significantly increasing road construction, cropland, and pasture – which, as indicated in the study, would further push the macaques and other animals to higher mountains.

4.3 Prospective geographical distribution and 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 2 and 3 demonstrate that macaques would be distributed in the southern and eastern Southwest, southeastern Northwest, and southeastern Coastal. Compared to the current profiles, the highly suitable distribution would be slightly increased referring to SSP2 but continue reducing considering SSP5 (Figure 3), implying that the greenhouse emission patterns would 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 (Figure 4) 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 S3, macaques are left out of such PA promotion: more than 87% of their suitable habitats from now on to the 2050s are not covered by Pas, indicating their conservation prospect is facing the challenge, and the implementation of the conservation strategies proposed (please see below) in this study is urgent.

On the other hand, migration corridors for the macaques would be noticeably reduced, referring to SSP2, corresponding to further fragmented habitats. Such passages would be more condensed in the southern Central, featured by shorter and isolated, considering SSP5 (Figure 5), indicating that their expected migration space would be further confined. That especially applies to some threatened taxa, such as the Arunachal macaque, distributed only in southeastern Tibet (Kumar et al., 2020), at the edge of extinction due to hunting and retaliatory killing in response to crop damage (Sinha et al., 2006). The other species having reduced habitats and less 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, a newly discovered in southeastern Tibet (Li et al., 2015).

According to Figure 5, 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 (Figure 5C). Besides macaques, other wildlife would be suffered 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 seven species' conservation situations are equally weighted. However, there is a 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:

1. *Macaca cyclopis* in Twain and *M. mulatta* in the mainland are featured by stable population sizes and broad distribution (the latter). Their main threat is the conflicts with humans for cropland feeding (Lu et al., 2018; Wu and Long, 2020).
2. *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).
3. *Macaca leucogenys, M. munzala* and *M. leonina* , whose biological and distribution issues are still less understood, with narrow distribution and small population sizes. 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).

4.4 Deficiency

This study is a preliminary try to systematically provides an evolutionary change procedure of geographic distribution of the macaques in mainland East Asia from the Pleistocene to the 2050s during the Quaternary, associated with remarkable climate and bio-human impact factors. MaxEnt models illustrate progressive changes based on geographic records of fossils and extant species. Evolutionarily, macaques reached their distribution peak during the Plietstoce in East Asia, including the Korean Peninsula, Taiwan, and Japan(Li et al., 2020). Thus, the available fossil records may not reveal their real distribution profiles in LIG and LGM (Figure S1 and Figure 1). On the other hand, the extant macaque species on mainland Eas Asia demonstrate a broad geographic distribution, and the MaxEnt model only projects the basal ecological niches based on present-only distribution points; thus, the current distribution profile (Figure 2A) of the creatures may be narrow than their natural dispersion. Moreover, because of the incredible variety in ecology, habitat, and conservation statuses, the geographical change and conservation models proposed for the 2050s (Figs. 2B and 2C) may not have represented their survival perspective shortly regarding a specific species within the genus.

5. Conclusion

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 on mainland East Asia, 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). Macaques' suitable distributions, initially concentrated in the Southwest, Central, and Coastal 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 in mainland China, 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 in China will provide valuable future shelters for the macaques and perhaps other animals, considering more migration corridors will be reserved there. Thus, those areas should be prioritized in their conservation.

Author Contributions

Haitao Wang, He Zhang, and Ruliang Pan conceived the ideas and designed the methodology; Hexian Zhang, Hao Pan, and Rong Hou collected the data; Kang Huang, Songtao Guo, and Pei Zhang analyzed the data; Haitao Wang, He Zhang, Baoguo Li, and Ruliang Pan led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary Data

The datasets supporting this article have been uploaded as part of the supplementary material.

Data availability statement

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).

Conflict of interest

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

This project was explicitly supported by research grants from China's National Natural Science Foundation (31730104). The American Society of Primatologists wild 'Saving Primates Where They Live' Partnership Award.

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