Differential response to climate change and human activities in three lineages of Sichuan snub-nosed monkeys (Rhinopithecus roxellana)

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Abstract

Aim: Determining the mechanisms by which climate change and human activities affect patterns of ecological specialization in different genetic units of the same species is crucial for developing local or regionally-based conservation solutions. This study uses species distribution models and genetic analysis to (1) identify the evidence of intraspecific differences in the population size and distribution of the three extant lineages of Sichuan snub-nosed monkeys (Sichuan/Gansu (SG), Qinling (QL) and Shennongjia (SNJ)) and (2) determine why some lineages have lower population numbers, a smaller geographical distribution, and are more threatened with extinction.

Location: China.

Methods: We used n-dimensional hypervolume modelling and genotype-environment association (GEA) models to compare the climatic niches of three snub-nosed monkey lineages, SDMs to reconstruct the historical, current and future distributions of each lineage and SMC++ to calculate their effective population sizes.

Results: We found evidence of: (1) climatic niche differentiation among the SG, QL and SNJ lineages of Sichuan snub-nosed monkeys; (2) geographical isolation combined with a decrease in population size during the LGM resulted in ecological specialization among these three lineages; and (3) a decline in climatic suitability and anthropogenically driven land conversion, combined with small population size and a narrow distributional range, indicates that the SNJ lineage is at a greater risk of extinction than the SG and QL lineages.

Main conclusions: We demonstrate that during the LGM a reduction in habitat suitability driven by climate change, in concert with decreasing population size, resulted in the geographical isolation of the three Sichuan snub-nosed monkey subpopulations, leading to lineage differences in ecological specialization. GEA models and hypervolume models demonstrated that the three lineages occupy different ecological niches. Based on lineage-level models, the SNJ and QL lineages should be the immediate focus of conservation efforts due to their small effective population size and expected...
Climate change, particularly during the Pleistocene, was an important factor affecting species richness, endemism, distribution, population persistence and the threat of extinction in many animal lineages (Daru et al., 2017; Nogués-Bravo et al., 2010; Sandel et al., 2011). More recently, climate change, along with changes in species interactions in response to anthropogenic habitat conversion, has resulted in local population extinctions, as well as species shifts in biogeography, population size, patterns of gene flow and subpopulation isolation (Chen et al., 2011; Lenoir & Svenning, 2015; Parmesan & Yohe, 2003). Niche conservatism assumes that sister taxa will continue to occupy similar ecological niches, whereas theories of niche divergence argue that over time, isolated populations of sister taxa will become more dissimilar in aspects of their behaviour, biology and ecology (Losos, 2008; Wiens & Graham, 2005). In response to changing environmental conditions, these individual populations may expand or contract their geographical distribution or adapt to local conditions (Franks et al., 2007). This can result in ecological specialization among isolated populations of the same species or the formation of new species. Elucidating the impact of expansions and contractions in species distribution provides a template for understanding the set of ecological and demographic challenges faced in responding to changing conditions (Louis et al., 2020). For example, climate oscillations during the penultimate ice age of the Pleistocene resulted in the red panda (Ailurus fulgens) splitting into two species (A. fulgens and A. styani). These two species differ in morphology and biogeography (Hu et al., 2020). In this regard, a fundamental goal of the study of conservation biology is to understand how changes in climate and ecology differentially affect the distribution, effective population size and local adaptations of subpopulations of a single species or sister species (Román-Palacios & Wiens, 2020).

Species distribution models (SDMs) represent a powerful tool for predicting a species' potential distributional range in response to changing environmental conditions (Araújo et al., 2005; Elith & Leathwick, 2009). A primary assumption of SDMs is “niche conservatism” (i.e., that species continue to exploit their ancestral niche even in the face of environmental change) rather than evolving new traits in response to changing environmental conditions. However, during extended periods of isolation or limited gene flow, subpopulations of the same species may alter their behaviour and biology in response to local environmental conditions (Soberón, 2007). Combining SDMs with genetic analysis can reveal intraspecific or sub-populational differences in range distribution as well as evidence of periods of population expansion and contraction (Pearman et al., 2010; Serra-Varela et al., 2015; Smith et al., 2019). In addition, using SDMs below the species level can help to explain the adaptive responses of different phylogeographic lineages to current and future environmental conditions, and provide a more accurate set of range estimates needed for the conservation management of threatened populations (Smith et al., 2019; Zhang et al., 2021).

Sichuan snub-nosed monkeys are an endangered primate species endemic to China (Li et al., 2002). Based on written records over the past 2000 years, this species was widely distributed across the provinces of Shaanxi, Henan, Hubei, Hunan, Guizhou, Guangdong, Guangxi, Fujian and Zhejiang, with its northernmost boundary reaching the North China Plain (Li et al., 2002; Zhao et al., 2018). At present, due to climate change and human activities resulting in habitat degradation, deforestation and the conversion of natural habitats into croplands, urban centres, road and rail networks, Sichuan snub-nosed monkeys are divided into three lineages or subpopulations distributed across only four provinces, Sichuan, Shaanxi, Hubei and Gansu. These three Sichuan snub-nosed monkey lineages are referred to as the Shennongjia (SNJ), the Sichuan-Gansu (SG) and the Qinling (QL) lineages. They differ in population size, distribution, craniofacial anatomy and adult sex ratio (Li et al., 2002; Zhao et al., 2018). Based on genomic data, the SNJ lineage appears to have diverged from the population that included the SG and QL lineages some 245,000 years ago. The split between the SG and QL lineages occurred during the onset of the Last Glacial Maximum, some 21–19 kya years ago (Kuang et al., 2019).

The SNJ population differs from both the SG and QL populations in possessing extremely reduced or absent nasal bones, fusion of the premaxilla superior to the piorform aperture, a longer tail and longer forelimbs (Kirkpatrick, 1998; Wang et al., 1998). Furthermore, although all three lineages are characterized by a modular or multi-level society in which several independent one male, multi-female plus offspring social units (OMUs) merge to form a large cohesive breeding band of up to several hundred individuals (Qi et al., 2014), the ratio of adult females to adult males in the OMUs varies from 4.27:1 in the QL lineage to 5.33:1 in the SG lineage, to 6.96:1 in the SNJ lineage (Zhu et al., 2021). Currently, the SNJ lineage has the smallest population size (1590–2180 individuals). By contrast, the QL lineage has a population size of 5240–5760 and the SG lineage has a population size of 15,880–18,190 individuals (Yu et al., 2022).
Today, these three lineages are separated by distances of hundreds of kilometres and appear to have been isolated for at least 10 kya (Kuang et al., 2019; Zhou et al., 2016).

Previous studies have used SDM models or genomic data to examine the effects of historical climate oscillation events on genetic differences and habitat suitability for Sichuan snub-nosed monkeys (Li et al., 2021; Zhou et al., 2016). However, none of these studies considered the possible effects that in situ ecological conditions, subpopulation isolation and local adaptation may have had on Sichuan snub-nosed monkey population demography and evolution. Thus, the degree to which each of the three Sichuan snub-nosed monkey subpopulations has differentially responded to changes in local environmental conditions remains unclear.

In this study, we examined evidence of ecological specialization among the three lineages of Sichuan snub-nosed monkeys based on a comparison of niche differentiation, climatic suitability (the geographical distribution of each population under different climatic conditions) and effective population size over the past 140–120 kya. We also assessed the response of each lineage to climate change using both species-level models and genetic lineage-level models. Our goals were to: (1) examine evidence of changing environmental conditions that led to the geographical isolation of the three lineages of Sichuan snub-nosed monkey (SG, QL and SNJ); (2) determine why some Sichuan snub-nosed monkey lineages have lower population numbers, a smaller geographical distribution, and are more threatened than others; (3) predict the future distribution of each lineage based on models of expected climate change and human activities over the next 30 years (from the present to the 2050s); and (4) offer a set of conservation strategies to prevent the extinction of populations of this endangered primate species.

## METHODS

### 2.1 | Species distribution data and predictor variables

Between 2016 and 2021, we carried out field surveys covering the entire current distribution of Sichuan snub-nosed monkeys across Sichuan, Gansu, Shaanxi and Hubei Provinces, China. We collected 723 current location records of Sichuan snub-nosed monkeys (Figure 1). At each location, we either visually documented or collected physical evidence (faeces) of Sichuan snub-nosed monkeys. In order to avoid resampling the same group, we excluded location points that were within 2 km of each other using the package “SpThin” (Aiello-Lammens et al., 2015). This distance represents the average home range centre between neighbouring groups of Sichuan snub-nosed monkeys reported in the literature (Hill & Winder, 2019). This procedure resulted in a final data set totalling 293 location records (223 location records for the SG lineage, 58 location records for the QL lineage and 12 location records for the SNJ lineage).

We obtained bioclimatic variables from WorldClim (http://www.worldclim.org/) and PaleoClim (www.paleoclim.org), which included climate data for the current period, future (2050), the last glacial maximum (LGM, 21–19 kya) and the last interglacial period (LIG, 140–120 kya). Future bioclimatic variables are based on the MIROC5 model under the RCP4.5 and RCP8.5 scenarios (RCP is the Representative Concentration Pathway; RCP8.5 represents greenhouse gas emissions without climate change policy intervention; RCP 4.5 represents greenhouse gas emissions assuming policy interventions). The spatial resolution of these data in the current and LGM periods is 30 arc-seconds. We resampled the spatial resolution of the LIG (2.5 arc-minutes) also to 30 arc-seconds. We focussed on

![FIGURE 1](image_url) The current distribution of the Sichuan snub-nosed monkey. The SG lineage of Sichuan snub-nosed monkeys is distributed in southern Gansu and northern Sichuan Province; the QL lineage is distributed in the Qinling area of Shaanxi Province; and the SNJ lineage is distributed in the Shennongjia area of Hubei Province.
climate variables associated with ‘ecological needs’ as factors affecting habitat suitability for Sichuan snub-nosed monkeys (Dong et al., 2019; Luo et al., 2015; Zhang et al., 2019). We then sorted these variables by importance and calculated Pearson’s correlation coefficients. When the correlation coefficient of the two variables was \(|r| > .7\) (Figure S1), we kept the variable that contributed most to the model and eliminated the least important variable (Dormann et al., 2013). Six climate variables were used in our analyses including Bio4 (Temperature Seasonality), Bio5 (Maximum Temperature of the Warmest Month), Bio6 (Minimum Temperature of the Coldest Month), Bio15 (Precipitation Seasonality), Bio18 (Precipitation during the Warmest Quarter) and Bio19 (Precipitation during the Coldest Quarter). In addition, we included human activities in the models, such as the total area of cropland, human population density (Popd) and the human footprint (Hfp) (HYDE3.2, Goldewijk models, such as the total area of cropland, human population density (Popd) and the human footprint (Hfp) (HYDE3.2, Goldewijk, 2017; Venter et al., 2016). All human activity data were resampled to maintain a consistent spatial resolution of 30 arc-seconds.

2.2 | Niche comparisons

The benefit of using lineage-level models is to identify differences in the realized niche among the SG, SNJ and QL lineages. To accomplish this, we verified whether the realized niche of the three lineages could be differentiated under filter predictors in the previous step. If there was differentiation, then we could use the lineage model. If there was no differentiation, then the lineage model could not be applied.

We next compared differences in the 6 climate variables across the three geographically isolated snub-nosed monkey subpopulations (SG, QL and SNJ) using n-dimensional hypervolumes in the R package hypervolume (Blonder et al., 2014, Blonder, 2018). We measured the resulting climate niche of each subpopulation based on these hypervolumes. We used the volume (unitless) of each hypervolume to measure the size of the realized niche under different predictors. The higher the number, the broader the potential ecological breadth of the species. Finally, we compared niche overlap and niche differentiation of the realized niche among the three lineages using the R package BAT (Cardoso et al., 2020; Carvalho & Cardoso, 2020; Zhang et al., 2021). The value of niche differentiation ranges from 0 (complete overlap) to 1 (complete separation).

2.3 | Species distribution modelling

We used MaxEnt 3.4.4 (Phillips et al., 2006) to develop species distribution models (SDMs) and simulated the historical (Model-historical, Model-hist) and current (Model-current, Model-curr) distributional range based on the geographical reference locations and the 6 climate variables that describe the spatial locations of Sichuan snub-nosed monkeys. MaxEnt is a presence-only algorithm (Elith et al., 2006; Phillips et al., 2006) and is widely used to simulate the distributional range of a species. The MaxEnt model projected the historical species distribution and future subpopulation distributions based on the relationship between their current distribution and environmental variables (Booth et al., 2014). Based on this relationship, the model predicted the historical and future distribution using historical and future climates. Considering that our data set is based only on occurrence records, we used 10,000 randomly generated background points to construct the SDMs (Elith et al., 2006). MaxEnt contains default settings that can produce overfitting models (Radosavljevic & Anderson, 2014); thus, we set up different combinations of models to evaluate, and we selected the best combination. We set up different feature combinations, which included linear (L), quadratic (Q), hinge (H) and regularization multipliers. The regularization multipliers ranged from 0.5 to 4, with an interval of 0.5 (Kass et al., 2021; Muscarella et al., 2014). We used the spatial cross-validation method to evaluate the robustness of the models. First, we divided the two longitudinal blocks and then divided the latitudinal blocks on that basis. We used three blocks for model training and used the fourth block to verify the model. We repeated this process until all four blocks were used as verification data (Silva et al., 2020). In addition, to compare the degree of environmental similarity between the training data and the validation data of each space block, we calculated multivariate environmental similarity surface (MESS) values using the rmaxent package (Baumgartner & Wilson, 2020; Elith et al., 2010) (Figures S2–S9).

To select the best model, we selected models with a minimum average of 10% omission rate, or the proportion of validation events whose fitness predictions were lower than the 0.1 quantile training predictions. Then, among multiple models with the minimum omission rate, we chose the highest average model validation training AUC (Kass et al., 2021). A higher AUC value (i.e., close to 1) indicates better model performance (Arias-Alzate et al., 2020; Lobo et al., 2008). Finally, we used the Boyce index, which ranges from −1 to 1 (values above 0 indicate good performance) to assess predictive abilities (Hirzel et al., 2006).

We used the “cloglog” output in the Maxent package (Phillips et al., 2017), converted the continuous output into binary with a training presence threshold of 0.1% and generated simulated habitat distribution maps (Zhang et al., 2021). We performed species-level models for four periods (LIG, LGM, Present and Future [RCP4.5 and RCP8.5]) and lineage-level models during two periods (Present and the Future).

2.4 | Population dynamics analysis and the genotype-environment association (GEA) method

SNPs used in our population dynamics analysis and GEA method were from Zhou et al. (2016). Given that one of the 27 individuals in Zhou et al.’s data set was located outside the range of our study areas, we deleted this individual and our data set therefore is based on genetic samples from 26 Sichuan snub-nosed monkeys including individuals from the SG lineage (13), the QL lineage (7) and the SNJ lineage (6). Unusable SNPs were excluded based on MSMC-tools advice (https://github.com/sstschiff/msmc-tools). In total, we analysed 117,110 SNPs (SG:13215; QL: 60911; and SNJ: 42984).

We used SMC++ to extrapolate the recent population history and the time of divergence of the three lineages (Schiffels & Durbin, 2014;
varimax rotation was applied to the PC axes maximizing the correlation between the axes and the SNPs. The resulting components and principal components (PCs) in R on the scaled data and the resulting algorithm that creates multiple decision trees. SNPs were ordinated by the relationship between each locus and the bioclimate variables, we ran

...resulted in 1,681,114 SNPs (filtering parameters: maf <0.05, min-meanDP = 5, max-meanDP = 50, max-missing = 1, hwe = 0.001, mInGQ = 20). To test the independence of individuals, we analysed kinship coefficients and inbreeding coefficients (F) for Sichuan snub-nosed monkeys (Figure S10). Our inbreeding coefficient results indicated that most individuals were not inbred (0 < F < =0.35) and that most individuals had kinship coefficients of 0. Then, we used SMC++ software to extrapolate the effective population size (Ne) of the three lineages of Sichuan snub-nosed monkey (Schiffels & Durbin, 2014). The mutation rate per generation per site was set as 1.36e-8 and the generation time was set to 10 years.

The genotype-environment association (GEA) method can identify adaptive loci by constructing the relationship between genetic and environmental data (Forester et al., 2018). To identify the relationship between each locus and the bioclimate variables, we ran a GEA model using Random Forest (RF), a machine-learning algorithm that creates multiple decision trees. SNPs were ordinated by principal components (PCs) in R on the scaled data and the resulting PCs were used in a parallel analysis (Forester et al., 2018). Then, a varimax rotation was applied to the PC axes maximizing the correlation between the axes and the SNPs. The resulting components and environmental variables were used as dependent and predictor variables, respectively. We retained the components that were significantly correlated with the constrained axis. Outliers that correlated with these retained SNP components were eliminated.

3 | RESULTS

3.1 | Differences between realized niches and climatic suitability

The volume of the five-dimensional hypervolume (defined as ecological niche space), which is an indicator that quantifies ecological amplitude, was largest for the SG lineage (2, 272) followed by the SNJ (42) lineage and the QL lineage (19). These data suggest that the SG lineage has the widest ecological range of each of the three subpopulations (Figure 2). Climate niche differences between any two subpopulations were 1.00 (SNJ: QL), 0.99 (SG: QL) and 1.00 (SG: SNJ) indicating a complete separation among these three isolated primate lineages in the set of climate factors that characterize their distributional range. The results indicated that Bio4 (Seasonal Variation in Temperature), Bio15 (Precipitation Seasonality) and Bio19 (Precipitation during the Coldest Quarter) contributed most to the differentiation between the SNJ and SG lineages and that Bio4 and Bio 19 contributed most to the differentiation between the SNJ and QL lineages (Figure 2).

Each of the models was characterized by a good performance, with high AUC values (ranging from 0.93 to 0.99) and continuous Boyce index values above 0 (Table 1; Figures S2–S9). The results of the species-level models showed that the area of climatic suitability for Sichuan snub-nosed monkeys decreased by 59.5% between the LIG and the LGM (Figure 3, a1-a2). By contrast, the area of climatic suitability expanded by 55.0% between the LGM and the present (Figure 3, a2-a3). Based on the species-level models, the availability of areas of suitable climate was expected to decrease by 36.6% (RCP4.5; RCP8.5:46.8%) in the future (Table 2, Figure 3, a3-a5).

Overall, the results indicated that the most critical variable affecting climatic suitability in the species model was Bio5 (maximum temperature during the warmest month of the year) (Table 2; Figure S7).

When considering human activities, the species-level models experienced a decrease of 19.2% in suitable habitats between the present and the year 2050, with an expansion of cropland contributing most to the model (Table 2, Figure 3, c1-c2). During these same periods, the lineage model predicted a 3.0%, 74.5% and 69.6% reduction in habitat suitability for the SG, QL and SNJ lineages, respectively (Table 2; Figure 3, d1-d2).

3.2 | SDM projections for the three lineages

The lineage-level models predicted a 76.7% (RCP4.5; RCP8.5: 57.9%) decrease in climate suitability for the QL lineage and an 80.2% (RCP4.5; RCP8.5: 93.6%) decrease in climate suitability for the SNJ lineage over the next 30 years (present to 2050). For the SG lineage, however, the model predicted a 5.6% increase in climate suitability over the same period (RCP4.5; RCP8.5: decreased by 17.8%; Table 2; Figure 3, b1-b2). Differences in the expansion or contraction of future habitat suitability for each Sichuan snub-nosed monkey lineage are best explained by local changes in rainfall. In the regions inhabited by the QL and SNJ lineages, the maximum temperature during the warmest month of the year is expected to increase by 1.2°C and the minimum temperature during the coldest month of the year is expected to decrease by 2.3°C over the next 30 years.

3.3 | Fluctuation in effective population sizes, Ne and divergence among the three lineages

Our results revealed that the three Sichuan snub-nosed monkey lineages independently experienced different demographic trajectories from the LIG to the present (Figure 4). The SG and QL lineages experienced a similar demographic history including two population bottlenecks and two small population expansions from the LIG to the present. The SNJ lineage, however, was characterized by a single population bottleneck and a single small population expansion from the LIG to the present. Between the LIG and the LGM, all three lineages experienced an initial increase in Ne, followed by a decrease. By contrast, between the LGM and the present, the Ne of the SG and
QL lineages initially decreased and then later increased. During this same period, the Ne of the SNJ lineage decreased (Figure 4).

SNPs of three lineages of Sichuan snub-nosed monkey indicated different climatic adaptations. SNPs adapted to the annual mean temperature, isothermality and precipitation during the driest month for the SNJ lineage. In the QL lineage, SNPs adapted to the annual mean temperature, temperature seasonality and the mean diurnal temperature. For the SG lineage, SNPs adapted to the annual mean temperature, annual precipitation and the mean range of diurnal temperature (Figure 4).

FIGURE 2 The hypervolumes for Sichuan snub-nosed monkeys including the Sichuan-Gansu lineage (SG), the Qinling lineage (QL) and the Shennongjia lineage (SNJ). Hypervolumes under Bio4 conditions with the SNJ lineage separating from the SG lineage, hypervolumes under Bio5 with the SNJ lineage separating from the SG lineage, hypervolumes under bio6 with the SNJ lineage separating from the SG lineage, hypervolumes under Bio6 with the SNJ lineage separating from the QL lineage, hypervolumes under Bio15 with the SNJ lineage separating from the SG lineage and the SNJ lineage separating from the QL lineage, and hypervolumes under Bio18 and Bio19 the three lineages not separating.

TABLE 1 Parameter settings and threshold value for Sichuan snub-nosed monkeys under species-level models and lineage-level models

| Model          | Feature | RM | Validation AUC | 10% omission rate (%) | Threshold | CBI | No. of nonzero model coefficients | AIC       |
|----------------|---------|----|----------------|------------------------|-----------|-----|----------------------------------|-----------|
| Species        | L LQ    | 3.5| 0.93 0.95      | 0.09 0.14 0.34 0.36    | 0.99 0.99 | 6   | 8                                | 7189 6553 |
| Lineage-SG     | LQ LQ   | 0.5| 0.95 0.95      | 0.11 0.13 0.2 0.32     | 0.99 0.98 | 10  | 8                                | 4848 4830 |
| Lineage-QL     | LQ LQ   | 0.5| 0.98 0.98      | 0.12 0.12 0.35 0.42    | 0.97 0.95 | 7   | 11                               | 1098 1090 |
| Lineage-SNJ    | L H     | 2.5| 0.98 0.99      | 0.25 0.25 0.51 0.54    | 0.61 0.65 | 1   | 24                               | 213 NA    |

Abbreviations: CBI, Continuous Boyce Index; CH, climatic variables and human activities; CL, climatic variables; H, hinge; L, linear; Q, quadratic; RM, regularization multiplier; Threshold, 10% omission suitability threshold.
The set of behavioural, biological, social and ecological factors that result in a species expanding or contracting its distributional range and population size under changing climatic conditions is a primary focus of conservation biology. In this study, we combined data on effective population size, climate suitability, GEA models and genetic lineage differences to develop SDMs models that explain how different lineages of the same species differentially adapted to local climatic conditions. Specifically, we found evidence of niche divergence among the SG, QL and SNJ lineages of Sichuan snub-nosed monkeys, and using lineages models identified the conservation threats facing each lineage.

### Ecological specialization among the three lineages

Using climatic suitability as a proxy for species distribution under climatic conditions, Sichuan snub-nosed monkeys were found to expand their range during warmer interglacial periods and then experience range contraction during the colder glacial periods (Figure 3). Fossil evidence suggests that during the Late Pleistocene and Early Holocene, Sichuan snub-nosed monkeys were more widely distributed across central and southern China (Gu & Hu, 1991; Han, 1982; Zhao et al., 2018). Today, Sichuan snub-nosed monkeys are found only in protected reserves in Gansu, Sichuan, Hubei and Shaanxi provinces (Li et al., 2002). A study by Quan and Xie (2002) reported that during the late Pleistocene, Sichuan snub-nosed monkeys were present at altitudes of 500–1400 m. By contrast, today, populations of this species are only found at altitudes from 800 to over 2500 m (Li et al., 2002; Quan & Xie, 2002). This suggests that either populations of this species have adapted to the colder, lower oxygen and extreme seasonal conditions that characterize high altitude temperate environments, possibly in response to selective pressures during the LGM, or that the low population numbers for the three subpopulations reflect this species inability to adapt well to high altitude habitats (Kuang et al., 2019; Yu et al., 2016; Zhou et al., 2014, 2016).

During the LIG, the Ne of Sichuan snub-nosed monkeys increased. However, beginning in the LGM, the three lineages appear to have diverged, coinciding with a decrease in Ne associated with range contraction (Figure 4). We found that with a reduction in climate suitability during the LGM, patterns of range expansion and contraction led to expansions and contractions in subpopulation demographic trajectories resulting in periods of geographical isolation (Figure 3). This scenario is confirmed by the results of genomic analysis indicating that the three lineages split around 10,000 years ago and then adapted to their respective local environmental conditions (Zhao et al., 2016). For example, each of the three lineages experienced different evolutionary changes in certain functional genes associated with hypoxia (Zhou et al., 2016). In addition, there also is evidence of differences in morphology and social structure that distinguish these three subpopulations that appear to be the result of subpopulation isolation over the past 10,000 years (Collart et al., 2021; Kirkpatrick, 1998; Li et al., 2003; Smith et al., 2019; Wang et al., 1998; Zhou et al., 2016; Zhu et al., 2021).

Our results based on GEA models indicated that temperature and precipitation had a significant effect on the genetic basis of local adaptations in the SNJ and SG lineages, whereas the SNJ lineage appears to have adapted to isothermality and the amount of precipitation during the driest month of the year. In the case of the SG lineage, there is evidence of SNPs adapted to annual

### Table 2 Distribution of Sichuan snub-nosed monkeys projected by species and lineage maxent models. LIG, last interglacial; LGM, last glacial maximum

| Model | Time            | Species | Area/km² | Important factor |
|-------|-----------------|---------|----------|------------------|
|       |                 | Species |          | CL | CH | CL | CH |
|       |                 | LIG     | 198,219  | –  | –  | Bio5 | –  |
|       |                 | LGM     | 80,195   | –  | –  | Bio5 | –  |
|       |                 | Current | 124,297  | 37,312 | Bio5 | Bio5 |
|       |                 | 2050-RCP4.5 | 78,795 | 30,149 | Bio5 | Bio5 |
|       |                 | 2050-RCP8.5 | 66,115 | –  | Bio5 | –  |
| Linages-SG | Current | 34,326 | 27,288 | Bio5 | Bio5 |
|           | 2050-RCP4.5 | 36,257 | 26,458 | Bio5 | Bio5 |
|           | 2050-RCP8.5 | 28,226 | –  | Bio5 | –  |
| Linages-QL | Current | 4595 | 4078 | Bio5 | Bio5 |
|           | 2050-RCP4.5 | 1071 | 1040 | Bio5 | Bio5 |
|           | 2050-RCP8.5 | 1935 | –  | Bio5 | –  |
| Linages-SNJ | Current | 3409 | 1813 | Bio6 | Bio6 |
|           | 2050-RCP4.5 | 674 | 552 | Bio6 | Bio6 |
|           | 2050-RCP8.5 | 219 | –  | Bio6 | –  |

Abbreviations: CH, climate variables and human activities; CL, climatic variables.
precipitation and the mean range of diurnal temperature. By contrast with the SNJ and SG lineages, only temperature-dependent variables had an effect on the genetic basis of local adaptations in the QL lineage (Figure 4). In Sichuan snub-nosed monkeys, local adaptations to temperature and or rainfall appear to have driven niche differentiation and genetic differences among the isolated subpopulations.

Between the LGM and the present, the population sizes of the SG and QL lineages declined slightly. However, during this same period, the population size of the SNJ lineage declined sharply.

**FIGURE 3** Habitat suitability for Sichuan snub-nosed monkeys projected by species-level models and lineage-level models under different scenarios. (a1-a5): species-level models under only climate scenarios; (b1-b3): lineage-level models under only climate scenarios; (c1-c2): species-level models under climate+human scenarios; (d1-d2): lineages-models under climate+human scenarios.
Years ago (g=10, μ=1.36×10^{-8})
The QL and SG lineages are primarily distributed in the Minshan Mountains and Qinling Mountains, which have been regarded as ‘cradles’ of endemism during glacial periods (Rahbek et al., 2019). These refugia likely served to buffer against a sharp decrease in Ne during range contraction. In addition, during the LGM, Sichuan, Shaanxi and Gansu Provinces (where the SG and QL lineages are presently distributed) were characterized by subtropical forests that provided suitable habitats for these populations. By contrast, during the LGM the region occupied by the SNJ lineage was characterized by temperate forests and grasslands, resulting in more severe range contraction (Hou et al., 2018). Therefore, we suggest that the reduction in Ne for the SNJ lineage coincided with a reduction in coniferous forests, an extended and more severe winter season and the formation of the Loess Plateau preventing a northward expansion of forested landscapes (Song et al., 2020). Historically, the Shennongjia region was isolated from the Minshan Mountains and the Qinling Mountains and can be regarded as a cryptic glacial refugium (Cheng et al., 2021). Thus, in response to significant range contraction and a genetic population bottleneck during the LGM, the SNJ subpopulation appears to have been isolated from other Sichuan snub-nosed monkey populations (Li et al., 2003; Luo, Liu, et al., 2012; Zhou et al., 2014, 2016). In fact, all three lineages experienced a Ne decline during this period, which is analogous to that found in several other sympatric species such as the giant panda (Ailuropoda melanoleuca) and the Chinese grouse (Tetrastes sewerzowi) (Song et al., 2020). Since the mid-Holocene, however, human activities associated with hunting and habitat conversion, especially in the Shennongjia area where human populations existed as early as the Palaeolithic, are likely to have resulted in the further population decline of the SNJ lineage (Yuan & Guo, 2015). For example, archaeological evidence indicates a major increase in large-scale smelting of copper and lead ores in the Dajiuhe Peatlands of the Shennongjia area during the Bronze Age. A large human presence in this area is likely to have led to centuries of habitat destruction, hunting and snub-nosed monkey population decline (Liu et al., 2021).

Today, the ecological range occupied by the SG lineage far exceeds that of the QL and SNJ lineages (Figure 2). We suggest that decreases in temperature and precipitation during the winter months contributed most to climatic and ecological distinctions that separate the SNJ lineage from both the SG and QL lineages. Moreover, the SG lineage contains approximately 70% of the total current population size of Sichuan snub-nosed monkeys and maintains the largest ecological range (Figure 2). Based on lineage-level models, the SG subpopulation is expected to increase slightly by 2050 (or decrease slightly under the RCP 8.5). By contrast, the area of suitable climate for the QL and SNJ lineages is expected to decline sharply by 2050 (Table 2; Figure 3).

4.2 | Conservation implications

Compared with models that only consider climatic conditions, by including the effects of human activities, our study found a significant decrease in the area of suitable habitat available to each of the three lineages of Sichuan snub-nosed monkeys. Evidence suggested that human activities such as the conversion of natural forests for expanding agricultural production, road, rail and infrastructure development, and human population increase have critically affected the habitat, behaviour and population size of Sichuan snub-nosed monkeys (Li et al., 2021). For example, increased human disturbance in the Shennongjia Nature Reserve resulted in one group of Sichuan snub-nosed monkeys increasing their day range by 42%–45% (Li et al., 2005). Thus, to protect Sichuan snub-nosed monkeys, human disturbance across their distributional range should be strictly controlled.

Compared with the species-level model, the lineage-level model more accurately reflected patterns of range contraction for each of the three Sichuan snub-nosed monkey lineages. We also note that the genetic diversity of the SNJ lineage is lower than that of the other two lineages, reducing its likelihood of survivorship to the end of the century (Li et al., 2007; Luo, Liu, et al., 2012; Luo, Pan, et al., 2012; Pan et al., 2009). We strongly recommend the establishment of protected forested corridors between Shennongjia National Park and the Badong Nature Reserve. These corridors will serve to increase connectivity and gene flow across the SNJ subpopulation (Chang et al., 2012; Luo, Liu, et al., 2012). Given its larger distribution and population size, we argue for the need to prioritize maintaining the genetic diversity of the SG subpopulation (Luo, Liu, et al., 2012). In the future, the SG population could be used as a reservoir to increase the genetic diversity of the QL and SNJ lineages. We hope that bringing scientific and public attention to the endangered status and conservation imperatives needed to protect these three lineages of the Sichuan snub-nosed monkeys will help save this and other threatened species in southwest China, the Qinling Mountains and Shennongjia from extinction.

Our results indicate that integrating genetic information with SDM modelling is an important tool for identifying the evolutionary, climatic and anthropogenic mechanisms that have differentially affected the population structure of animal lineages and for designing effective programs for the survivorship of threatened species (Zhang et al., 2021). We found that climate suitability for all three lineages of Sichuan snub-nosed monkeys contracted during the LGM, and the effective population size of the SNJ lineage declined significantly after the LGM. This resulted in geographical and genetic isolation of individual subpopulations (Figure 4). Moreover, integrating species lineage-level models, species models and data on effective population size provides a quantitative and predictive basis for assessing the evolutionary history and conservation status of distinct populations of a single species.
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CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT
Presence records of the Sichuan snub-nosed monkey are presented in Dryad (https://doi.org/10.5061/dryad.dv41ns129). Environmental predictors are presented in online databases (See details in Methods).

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