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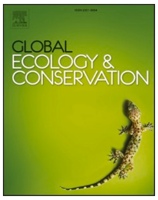

Spatiotemporal variation of anthropogenic drivers predicts the distribution dynamics of Hainan gibbon

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ABSTRACT

Understanding the historical causes of species endangerment is vital, yet difficult. The Hainan gibbon *Nomascus hainanus* has declined in numbers dramatically in the last century, resulting in a single population on Hainan Island in China. The lack of historical surveys has limited our understanding of habitat requirements and habitat loss, impeding an evidence-based approach to the conservation management of this species. Here, we used a variety of data sources, including literature, surveys, and expert experience, to reconstruct the historical distribution of Hainan gibbons and used a species distribution model (SDM) to predict suitable habitats in the 1950 s, 1970 s, and the 2010 s. We found that four anthropogenic drivers, namely human disturbance and habitat transformation, natural forest cover, landscape shape index, and distance to the nearest roads, played important roles in the distribution of the species (sum of their permutation importance >50%). The SDM based on earlier occurrences (1950 s) identified more suitable habitats than the model using recent data (1970 s), which supported the shifting and shrinking of the realised niche, as revealed by the probability density curves and niche hypervolumes. In addition, 89.29% of the distribution of Hainan gibbons revealed by historical occurrences was lost between the 1950 s and 2010 s, which was much faster than the habitat loss predicted by the SDM using the 1950 s (49.62%) or the 1970 s data (78.21%). Moreover, we recorded 108 individuals of Hainan gibbons harvested from the 1950 s to the 1980 s, of which 87.96% were hunted in the 1960 s, indicating severe damage to this species. Our study highlights the critical importance of using historical data to reconstruct the habitat requirements of species. We also suggest that spatially explicit habitat recovery and strict elimination of human disturbances should be undertaken in the Hainan Tropical Forest National Park, and corridors should be developed among isolated habitat patches to restore this species.

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1. Introduction

Understanding how the endangerment of a species is caused by anthropogenic factors is critical for maximising the effectiveness of conservation interventions (Bryant et al., 2015). Habitat loss, degradation, and harvesting are the main threats to mammals worldwide (Schipper et al., 2008). Primates are likely to have been affected by rapid changes and extreme events as they mostly lived in tropical areas with climatically stable environments since the start of the Holocene (Corlett, 2012; Pacifici et al., 2017). In addition, primates generally have slow life histories and reproductive rates, occur in large, noisy groups, and have relatively large bodies, making them especially vulnerable to hunting (Kalbitzer and Chapman, 2018; Linder and Oates, 2011). Alarmingly, approximately 60% of the world's primate species are threatened by extinction, and approximately 75% have declining populations owing to growing anthropogenic pressures and emerging threats, such as climate change and anthroponotic diseases (Estrada et al., 2017; Zhang et al., 2019). However, determining the extent to which these factors have caused the population decline may be particularly difficult for a species of extreme rarity because of the lack of historical distribution data and the difficulty of quantifying anthropogenic drivers.

In this context, mining data from multiple sources and applying them judiciously based on their varying reliabilities are key to the successful prediction of historical distribution. On the other hand, species distribution models (SDM) such as the maximum entropy model (MaxEnt), have been proven to be useful for predicting distributions across landscapes, even with as few as five observations, which is typical for rare species (Elith et al., 2006; Elith and Leathwick, 2009; Hernandez et al., 2006; Pearson et al., 2007). Occurrences should be matched with environmental variables in the corresponding periods when modelling distribution is affected by anthropogenic range contraction to avoid overpredictions of contemporary distribution or underpredictions of historical distribution (Pang et al., 2022). The niche reduction hypothesis states that novel threats to a species may not be uniform over the species' realised niche (Hutchinson, 1957), thus leading to reduced niche hypervolume and range reduction (Alexander, Cosentino, and Schooley, 2022; Scheele et al., 2017). Therefore, a complementary focus on reductions in the realised niche breadth of species will be more informative for understanding the processes driving species declines and developing conservation strategies than simply focusing on geographic patterns (Scheele et al., 2017).

The Hainan gibbon *Nomascus hainanus*, which is the most endangered gibbon, consists of a single population of 36 individuals restricted to the Bawangling National Nature Reserve (BNNR) on Hainan Island, China (Schwitzer et al., 2017; Yang and Hu, 2022). This species is distributed in forested areas across the island (Yan, 2008). The population has probably suffered bottlenecks since the 19th century and even further into the 20th century (Bryant et al., 2016). It was estimated to be approximately 2000 individuals in the 1950 s and may have dropped to as low as 7–8 individuals in 1980, primarily due to hunting and habitat loss (Jiang, 1996; Liu et al., 1984). Furthermore, the population recovered to 21 gibbons restricted to a 16 km^2 primary forest in 1989, subsequently fluctuated and was reduced to 13 gibbons in 2003 (Chan et al., 2005; Liu et al., 1989; Wang, 1995; Wu et al., 2004). Fortunately, the population has increased gradually since 2003, reaching a population of 36 gibbons by 2022 (Fellowes et al., 2008; Liu et al., 2022; Schwitzer et al., 2017; Schwitzer et al., 2015; Yang and Hu, 2022). The Chinese government established the Hainan Tropical Forest National Forest (HTFNP) in 2021, which provides opportunities for habitat restoration for the Hainan gibbon.

To develop an effective conservation strategy for this species, it is necessary to understand its habitat requirements and estimate the contraction of its realised niche under anthropogenic threats as well as the distribution of potential habitats for rejuvenation.

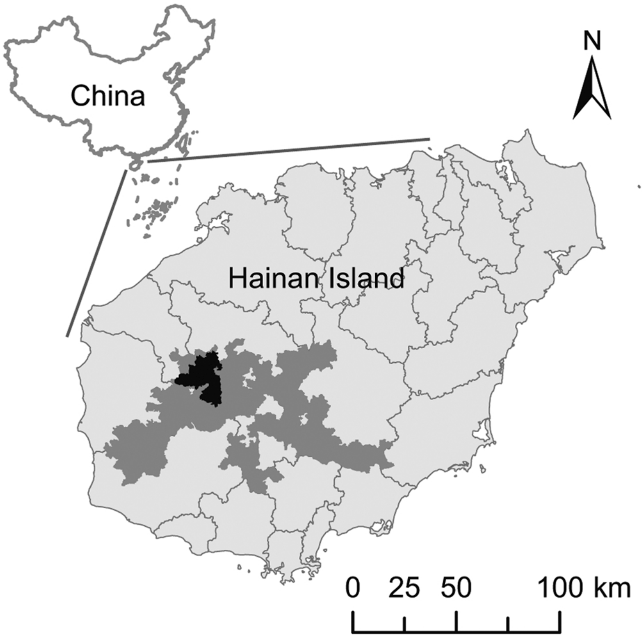

Fig. 1. The location of Bawangling National Nature Reserve (black) and Hainan Tropical Forest National Park (grey) on Hainan Island, China.

Nevertheless, the extreme scarcity of records of the Hainan gibbon in history, the habitat status, and uncertainty regarding the species' basic biology have previously impeded an evidence-based approach for the management of the population. Here, we constructed a dataset of historical Hainan gibbon occurrences based on our field surveys, expert experiences, and documents. MaxEnt was used to explore the effects of key anthropogenic drivers on this species, and Hutchinsonian niche hypervolumes (Blonder et al., 2018) were used to determine whether there was a reduction in the realised niche over time. We aimed to1) reconstruct the temporal changes in the spatial distribution of Hainan gibbons from the 1950 s; 2) estimate the effects of anthropogenic drivers on the habitat change of Hainan gibbons; and 3) detect the potential habitats of Hainan gibbons across Hainan Island and their limiting factors in HTFNP. This study will serve to generate new tools to support the ongoing conservation efforts for this highly threatened species.

2. Methods

2.1. Study area

Hainan Island is located at the northern edge of the Indonesia-Malay tropical zone, south of mainland China (Fig. 1). The topography of the island is composited with plains in the periphery and mountains in the middle with a highest altitude of 1867.1 m. Affected by the monsoon tropical climate, Hainan has an annual average temperature of 22–26 ℃, with 25–29 ℃ in the hottest months (July and August), and 16–21 ℃ in the coldest months (January to February). The annual precipitation is 1500–2000 mm, but changes from 275 mm in the west to approximately 3000 mm in the mountainous areas in the east, and more than 70% of the annual precipitation occurs from May to October.

The main vegetation type on Hainan Island is of the tropical rainforest type, dominated by Lauraceae, Euphorbiaceae, and Rubiaceae families with the most number of species, whereas Dipterocarpaceae, Sapindaceae, Sterculiaceae, and Ebenaceae have the most number of individuals in the forest (Zhu, 2017). The vegetation in Hainan has vertical zonality: mountainous areas with high rainfall encompass lowland rainforests below 600ḍ m, montane and ravine rainforests from 600 to 1200 m, and evergreen broadleaf forest above 1200 m, while small areas of dwarf mossy forests are distributed on ridges or mountain tops (Zhang et al., 2010).

2.2. Historical occurrences of Hainan gibbon

A dataset of 69 historical gibbon occurrence records with the numbers of Hainan gibbon harvested during 1868–2022 was compiled from multiple data sources, including:1) documents from Swinhoe (1870), Allen (1938), Tang and Li (1957), Guangdong Institute of Entomology and Sun Yat-sen University (1983), Song et al. (1999), FarmandBotanic Garden, 2001, and Bawangling Forestry Bureau (1983); 2) field surveys from the second survey of terrestrial wildlife resources of China, and surveys from South China Normal University (SCNU) in 2012; and 3) expert experiences of Prof. Haisheng Jiang from SCNU, who is Zhenhe Liu's successor at South China Institute of Endangered Animals and has studied Hainan gibbon from the mid-1980 s (Chan et al., 2005). The number of harvested gibbons was recorded. To successfully integrate multiple data sources, we carefully considered their spatial resolutions and differences in data collection methods, as previously suggested by Fletcher et al. (2019). Among them, only one occurrence had definite coordinate information; 14 occurrences were noted with local place names, 50 were located in villages or towns, and four were located in counties or cities (Appendix 1, Table S1). We then located all occurrence records on the map based on our knowledge and experience from questionnaires conducted by Zhenhe Liu et al. (1978, unpublished data) and Haisheng Jiang et al. (1998 and 2011, unpublished data) and related surveys conducted by Liu et al. (1984), Song et al. (1999), Bosco P.L. Chan et al. (2003, unpublished data), and Haisheng Jiang et al. (2015, unpublished data) in Hainan, as well as the 2012 monitoring data from the BNNR.

This dataset was further used to reconstruct historical distributions and prepare occurrence samples for the SDM simulations. To eliminate the potential bias in space and tolerate the maximum spatial uncertainty of the occurrences, we first divided Hainan Island into 5 km × 5 km grid cells and then used the grids that overlapped with at least one occurrence to represent the historical distributions of the Hainan gibbon. We removed redundant records that occurred in a single grid cell, resulting in 28 occurrences in the 1950 s and 19 occurrences in the 1970 s for the SDM simulations (Appendix 1, Table S2). This subsampling method reduces the spatial aggregation of records and could also underestimate the contribution of suitable areas where high records reflect the true ecological value for the species, but has been proven to be a competitive method for correcting sampling bias (Fourcade et al., 2014). Furthermore, we constructed a dataset of the population dynamics of Hainan gibbons since 1950 based on literature review (Appendix 2, Table S3).

2.3. Environmental variables

We produced the historical natural forest distribution (NFD) in the 1950 s and 1970 s by digitizing two sets of paper topographical maps made during 1958–1960 (1:250000) and 1975 (1:50000) in ArcGIS 9.3 (ESRI, 2008) using the methods described by Lin et al. (2017) (details in Appendix 3, Table S4). In this study, natural forests included arboreal forests, shrublands, and open woodlands formed by natural seeding or sprouting (PRC, 2011). The NFD in the 2010 s was reproduced from maps of the 8th National Forest Resources Inventory of China (http://www.forestry.gov.cn/gjslzyqc.html) and validated using field investigation data from 2012/2013 (overall accuracy=83.2%) (Xu et al., 2017). We then overlaid those NFDs with the 5 km × 5 km grids to calculate the natural forest cover (NFC) and a landscape shape index (LSI) for 1950 s, 1970 s, and 2010 s. The LSI can be used to evaluate the characteristics of interior and edge habitats for wildlife (Ripple et al., 1991) and was calculated using FragStats4.2 (McGarigal and Marks 1995) using formula (1), where P_i and a_i indicate the perimeter and area of natural forest patch i respectively, and n indicates the number of natural forest patches.

$$\frac{\sum_{i=1}^{n} \frac{0.25P_i}{\sqrt{a_i}}}{n} \tag{1}$$

Historical road networks of Hainan Island in 1950 s, 1970 s, and 2010 s, including expressway, highway, simply-built highway, cart road, and rural road, were obtained from Lin et al. (2017) (Appendix 3, Table S4). We then calculated the Euclidean distance to the nearest roads (ED_road) for the 5 km × 5 km grids to indicate related human disturbances.

Two topographic variables, elevation and slope, were calculated using a digital elevation model (DEM; http://www.gscloud.cn/; accessed on 21 September 2022). A soil-type map (hereinafter soil_type) with a 1 km resolution was downloaded from the Resource and Environment Science and Data Center, Institute of Geographic Sciences and Resources, Chinese Academy of Sciences (https://www.resdc.cn/data.aspx?DATAID=145, accessed on 15 Feb 2023). We differentiated soil type based on the level of order rather than group because the spatial heterogeneity of the soil group was too high for our limited sampling, and it is likely to be modified by land-use changes. Therefore, the landscape was classified into seven types: semi-eluvial, primary, semi-hydrous, saline-alkali, anthropogenic, ferruginous bauxite, and non-soil. Because temperature and precipitation can affect the phenology of trees of gibbon food species and thus affect gibbon fitness (Bach et al., 2017; Du et al., 2020), we used 19 WorldClim bioclimatic variables (BIO 1–19, version 2, http://www.worldclim.org, accessed on 21 September 2022) in our simulations. These 22 environmental variables were resampled to 5 km × 5 km resolution and assumed to be stable from 1950 to 2010.

We then calculated the correlation coefficients for the above 24 continuous variables using a spatial analyst tool in ArcGIS, and removed one of the two variables that were highly correlated ($|\text{correlation coefficients}| > 0.7$) with each other, and retained the one that is biologically important for the distribution of Hainan gibbon. Therefore, 10 variables were retained for further simulations, including elevation, slope, soil_type, NFC, LSI, ED_road, BIO2 (mean diurnal range), BIO4 (temperature seasonality (standard deviation ×100)), BIO6 (minimum temperature of the coldest month), and BIO12 (annual precipitation). In addition, we compared 10 environmental variables between gibbon occurrences and areas with hunting records from the 1950 s to the 1980 s to explore the potential impacts of hunting on gibbon distribution. The variables for the 1960 s and the 1980 s were assumed to be the same as those for the 1950 s and the 1970 s, respectively.

2.4. Simulation of suitable habitats

MaxEnt software (version 3.4.3, http://biodiversityinformatics.amnh.org/open_source/maxent/, accessed on 30 November 2020) to predict suitable habitats for Hainan gibbons. Initially, we ran a preliminary simulation and checked the reasonableness of the response curves for all 10 variables. We found that elevation showed a misleading response curve that excluded the Hainan gibbons from the lower elevations. In fact, Hainan gibbons were found at low elevations (<200 m) in the middle of the19th and early 20th centuries (Liu et al., 1984; Yan, 2008). Our dataset of historical gibbon occurrences also supported the presence of this species at low elevations (Appendix 4, Fig S1). This is similar to the historical distribution of Cao-vit Gibbon (*Nomascus nasutus*) (50–900 m) (Rawson et al., 2020), and other gibbons inhabiting tropical forest, such as East Bornean Grey gibbons (*Hylobates funereus*) (~ 180 m) in Sabah, Malaysia (Inoue et al., 2016), hoolock gibbons (*Hoolock leuconedys*) in Lawachara (22 m) and Chunati (15 m) (Ahsan, 2001). However, historical hunting and lowland forest transformation in the 20th century removed the Hainan gibbon from elevations < 700 m and gentle slopes (Chan et al., 2005; Zhou, 2008), which resulted in misleading response curves when elevation, slope, and their collinear variables (i.e., BIO1) were added as environmental variables in the SDM modelling. Therefore, rather than directly using elevation and slope in the modelling, we developed an index, HDT, to indicate the level of human disturbance and habitat transformation in the second half of the 20th century. We reclassified elevation and slope into eight and five classes, respectively, and multiplied them to obtain the HDT (Appendix 5, Table S5). This step resulted in nine variables for simulation: HDT, NFC, LSI, ED_road, soil_type, BIO2, BIO4, BIO6, and BIO12.

Finally, we developed predictive models using different combinations of occurrences and environmental variables:1) Model *a*, using 28 grid occurrences and nine environmental variables in the 1950 s; 2) Model *b*, using 19 grid occurrences and nine environmental variables in the 1970 s. We then used these two predictive models individually to predict habitats in the 1950 s, 1970 s, and the 2010 s using the corresponding environmental variables. We used only hinge features in Maxent because it can produce smooth models (Elith et al., 2010), thereby improving model performance without significantly increasing model complexity (Phillips and Dudik, 2008). We used default settings for features and regularisation for model training and ran the model 10 times using a cross-validated type (Merow et al., 2013). Subsequently, a threshold selection method to maximise the sum of sensitivity and specificity (Max SSS) was used to separate continuous habitat suitability into binary suitable or unsuitable habitats, as previously recommended (Liu et al., 2013). In addition, we evaluated the overall model performance using a receiver operating characteristic (ROC) curve analysis, which characterises the performance of a model at all possible thresholds using the area under the curve (AUC) (Phillips et al., 2006). A random prediction should result in an AUC value of 0.5, whereas a perfect classifier should have an AUC value of 1 (Phillips and Dudik, 2008). Furthermore, we ran a limiting factor analysis based on the smoothened MaxEnt model to detect the variable whose value most influenced model prediction (Elith et al., 2010).

2.5. Niche shifting

In order to determine the niche shifting of Hainan gibbon since 1950 s, we firstly compared the probability density curves (plotted

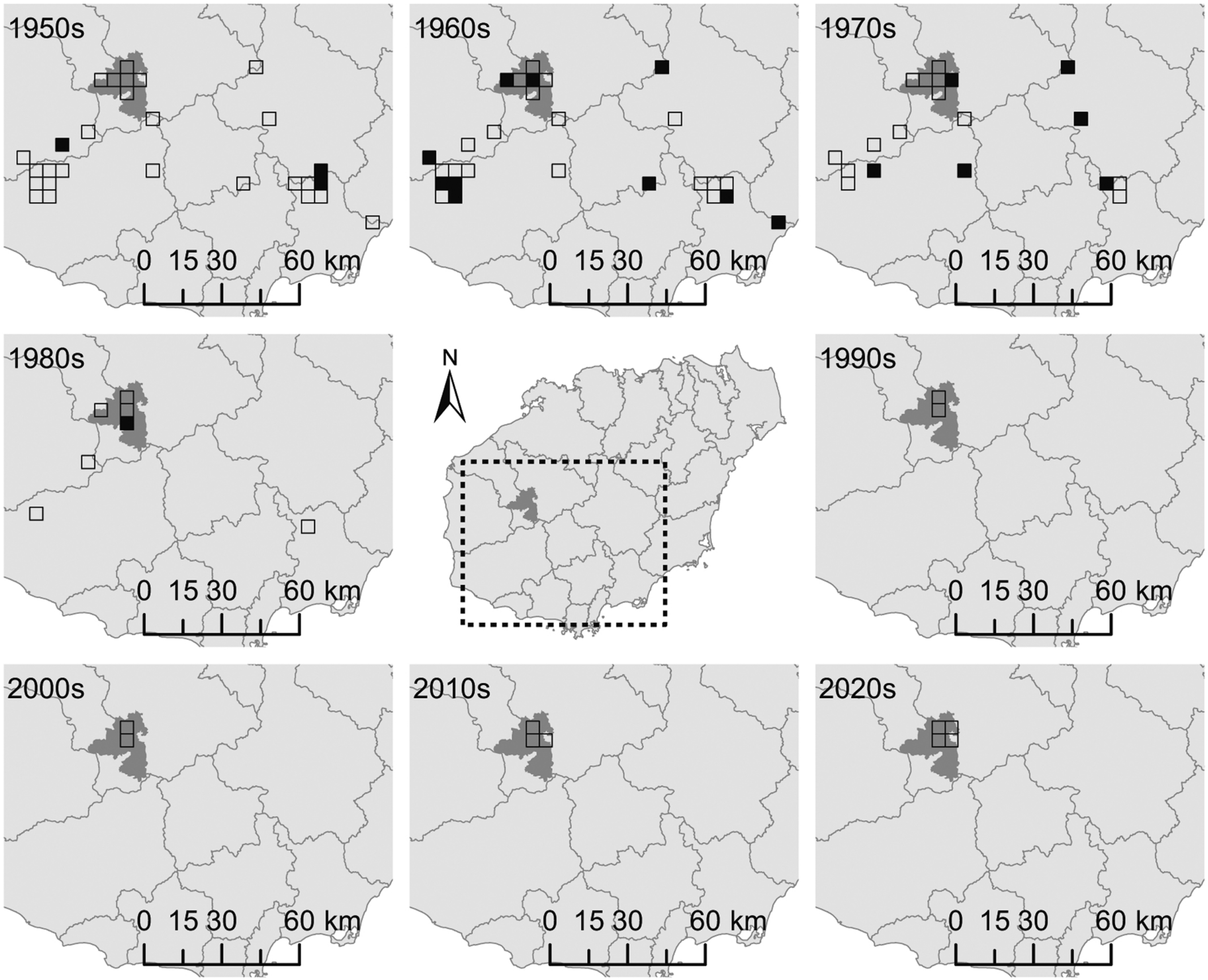

Fig. 2. Historical distribution of Hainan gibbon on Hainan Island, China. The blank grids indicate presence of Hainan gibbon in that area, while the filled grids indicate the incidences of gibbon hunting. The light grey indicates counties of Hainan whereas dark grey indicates the Bawangling National Natural Reserve (BNNR).

using the "*geom_density*" function of R package "ggplot") of the nine environmental variables used in the SDM; and secondly calculated niche hypervolumes in 1950 s and 1970 s using a one-class support vector machine (SVM) method (with the default values $\nu = 0.01$ and $\gamma = 0.5$) of the "hypervolume" package (Blonder et al., 2018). The SVM method was used because hypervolumes with different numbers of data points have the same overall sampling effort, allowing for outlier inclusion while generating a smooth boundary around the data and facilitating comparisons between time periods (Takach et al., 2020). We did not calculate the niche hypervolume in the 2010 s because there were only three occurrences during this period. Finally, we calculated the difference between the 1950 s and the 1970 s hypervolumes using one overlap (Sørensen–Dice similarity) and one distance (centroid distance) metric, as recommended (Mammola, 2019), to measure changes in the ecological niche for Hainan gibbons.

3. Results

3.1. *Distribution shrinking since 1950 s*

In the 1950 s, Hainan gibbons had a wide but scattered distribution across the southern part of Hainan Island, including 28 grids in which gibbons were documented to occur (Fig. 2). The distribution experienced a slight shrinkage during the 1960 s (27 grids) and then dropped sharply from 19 grids in the 1970 s to seven grids in the 1980 s and two grids in the 1990 s. Subsequently, its distribution recovered slowly and increased to four grids in the early 2020 s; however, this occurred only in the BNNR.

We found records that 108 Hainan gibbons had been harvested between the 1950 s and the 1980 s. Among these, 87.96% were hunted during the 1960 s, 7.41% were hunted during the 1970 s, and two individuals were hunted in 1980 (Appendix1, Table S1). Our data revealed that approximately one-third of the occurrence grids reported hunting of gibbons during the 1960 s and the 1970 s (Fig. 2). Gibbons were harvested from only three grids during the 1950 s, owing to a lack of information from earlier periods. From the 1950 s to the 1980 s, these occurrence grids had higher elevation and lower LSI and BIO6 than grids that had hunting records, but the difference was not significant (Table 1).

3.2. *Influences of environmental variables on Hainan gibbon distribution*

All models had an AUC > 0.9, indicating good performance of those simulations (Table 2). Model *a* performed better, predicting higher percentages of occurrence grids, than Model *b* when extrapolating to the other two periods. The most important variables (sum of their permutation importance (PI) > 90%) affecting gibbon distribution were HDT (PI=33.7%), BIO6 (33.2%), LSI (20.2%), and BIO2 (8.5%) in Model *a* and NFC (50.2%), BIO6 (29.7%), HDT (8.9%), and BIO 2 (7.3%) in Model *b*. Four anthropogenic factors (HDT, NFC, LSI, and ED_road) had a total PI of > 50% in both models. In addition, the response curves of the variables were similar between the two models and showed that, Hainan gibbons were more likely to be present at areas with HDT < 25, NFC > 70%, BIO6 < 14 °C, LSI < 1.5, BIO2 < 7 °C, ED_road > 2000 m, and ferruginous bauxite soil (Appendix 6, Fig S2).

Table 1

A comparison of 10 environmental variables in the areas of gibbon occurrences and areas from where gibbons were harvested during 1950 s~1980 s. NFC, LSI, ED_road, BIO2, BIO4, BIO6, BIO12, and soil_type indicate the natural forest cover, the landscape shape index (Ripple et al., 1991), the Euclidean distance to the nearest road, mean diurnal range, temperature seasonality (standard deviation ×100), minimum temperature of coldest month, annual precipitation, and the type of soil, respectively. There were no significant differences (P > 0.05) between the occurrences and the hunting areas for all the variables in the four periods.

Variables	Records	1950 s	1960 s	1970 s	1980 s
Elevation (m)	Occurrences	700.5 ± 44.9	710.3 ± 45.5	725.7 ± 63.5	754.6 ± 94.2
	Hunting areas	517 ± 151.7	696.3 ± 74	660.3 ± 125.9	662 ± 0
Slope (°)	Occurrences	20.7 ± 1.8	21.1 ± 1.8	20.9 ± 2.2	28.2 ± 3.8
	Hunting areas	20.0 ± 4.7	20.5 ± 2.7	16.3 ± 2.9	40.9 ± 0
NFC (%)	Occurrences	90.9 ± 3.0	92.2 ± 2.9	92.5 ± 1.8	93.9 ± 2.4
	Hunting areas	84.4 ± 13.6	94.2 ± 1.9	89.4 ± 4.4	87.7 ± 0
LSI	Occurrences	1.17 ± 0.05	1.16 ± 0.05	1.87 ± 0.16	1.75 ± 0.29
	Hunting areas	1.17 ± 0.11	1.23 ± 0.11	2.16 ± 0.34	3.27 ± 0
ED_road (m)	Occurrences	6517.1 ± 904.9	6719.6 ± 915.2	1847.6 ± 489.0	1166.6 ± 304.1
	Hunting areas	2201.0 ± 781.8	6847.4 ± 1739.8	2222.9 ± 715.4	1728.9 ± 0
BIO2 (℃)	Occurrences	6.7 ± 0.0	6.7 ± 0.0	6.7 ± 0.0	6.7 ± 0.1
	Hunting areas	6.8 ± 0.1	6.7 ± 0.1	6.8 ± 0.1	6.8 ± 0
BIO4	Occurrences	329.2 ± 2.8	329.5 ± 2.9	333.5 ± 3.2	334.9 ± 5.8
	Hunting areas	325.1 ± 7.2	326.9 ± 5.1	330.6 ± 6.6	346.8 ± 0
BIO6 (℃)	Occurrences	12.9 ± 0.2	12.8 ± 0.3	12.5 ± 0.3	12.5 ± 0.5
	Hunting areas	13.8 ± 0.1	13.0 ± 0.5	12.6 ± 0.6	13.1 ± 0
BIO12 (mm)	Occurrences	1649.9 ± 32.0	1645.7 ± 33.0	1638 ± 42.6	1634.3 ± 46.1
	Hunting areas	1655.7 ± 144.9	1647.5 ± 49.7	1675.2 ± 92.2	1603 ± 0
Soil_type	Occurrences	Ferruginous bauxite	Ferruginous bauxite	Ferruginous bauxite	Ferruginous bauxite
	Hunting areas	Ferruginous bauxite	Ferruginous bauxite	Ferruginous bauxite	Ferruginous bauxite

Table 2
Performances of the two MaxEnt models developed for predicting the habitat of Hainan gibbon in 1950 s, 1970 s, and 2010 s.

Model	Environmental variables	Time of input data for model development	AUC	Threshold for suitable /unsuitable habitat	Percentage of occurrence grids predicted by the model (%)		
					1950 s	1970 s	2010 s
a	HDT, NFC, LSI, ED_road, Soil_type, BIO2, BIO4, BIO6, BIO12	1950 s	0.918 ± 0.041	0.2128	92.86	78.95	33.33
b		1970 s	0.929 ± 0.044	0.3323	75.00	84.21	0

*HDT, NFC, LSI, ED_road, BIO2, BIO4, BIO6, BIO12, and soil_type indicate the levels of human disturbance and habitat transformation, the natural forest cover, the landscape shape index, the Euclidean distance to the nearest road, mean diurnal range, temperature seasonality (standard deviation ×100), minimum temperature of the coldest month, annual precipitation, and soil type, respectively.

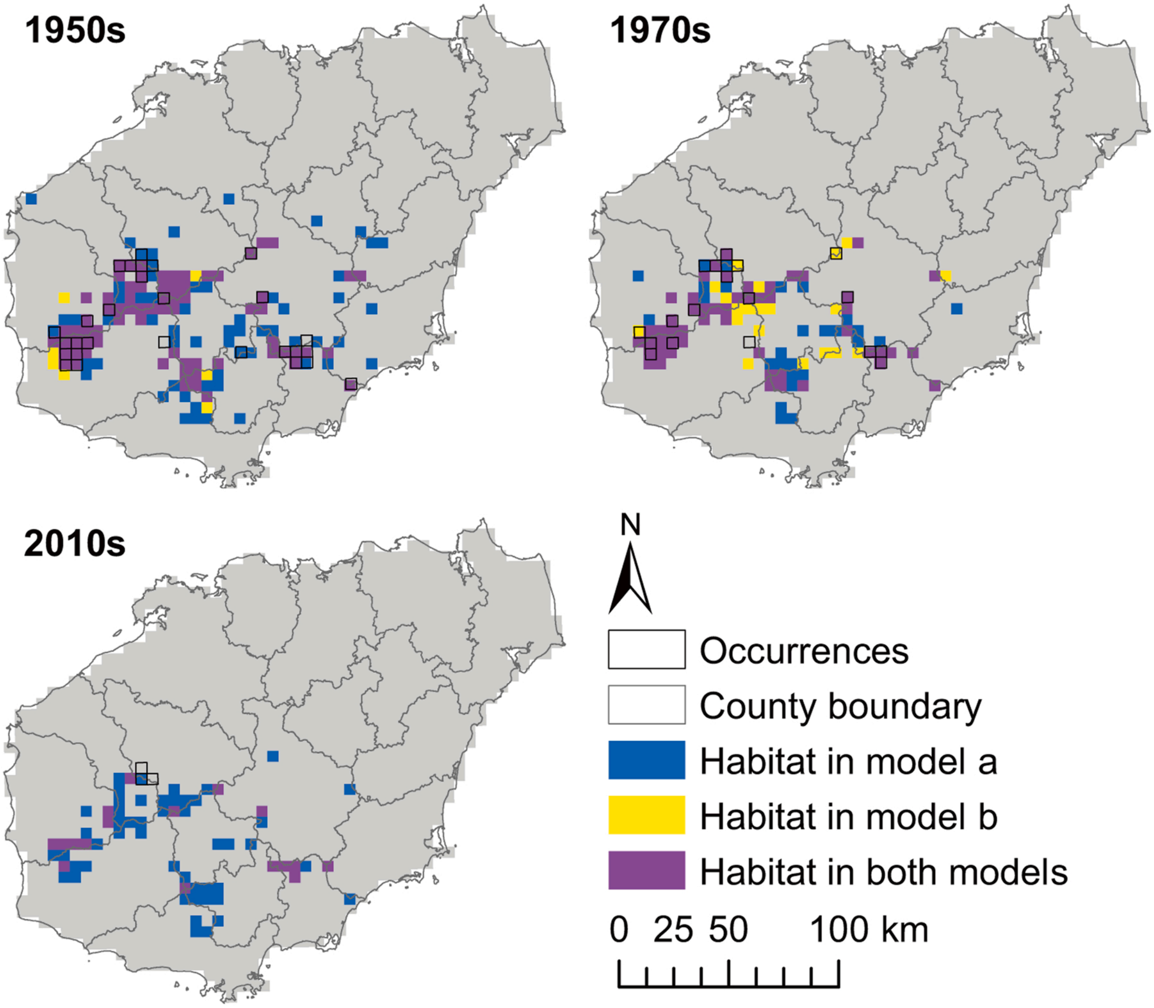

Fig. 3. Potential habitat of Hainan gibbon (*Nomascus hainanus*) in the 1950 s, 1970 s, and 2010 s on Hainan Island predicted by the MaxEnt using 1950 s data (model *a*) and 1970 s data (model *b*) respectively.

3.3. *Dynamics of suitable habitats*

The suitable habitat of the Hainan gibbon was predicted to decline from 3275 km^2 in the 1950 s to 1975 km^2 (60.31%) in the 1970 s and to 1650 km^2 (50.38%) in 2010 s by Model *a*. Model *b* predicted a much smaller habitat in the three periods, i.e., 1950 km^2, 1800 km^2, and 425 km^2 in the 1950 s, 1970 s, and the 2010 s, respectively (Fig. 3). In addition, our results showed that habitat suitability in most areas of the HTFNP in the 2010 s was primarily limited by the LSI, whereas some of the edges were mainly limited by the HDT (Fig. 4).

3.4. *Niche shifting since 1950 s*

There were shifts in the probability density curves for the environmental variables from the 1950 s to the 2010 s, except for the soil_type, where the gibbons were exclusively present in the area with ferruginous bauxite (Fig. 5, the result for soil_type is not shown). The grids with occurrences in the 1970 s had smaller ED_roads ($P < 0.01$) and higher LSI ($P < 0.01$) than those in the 1950 s. There were shifts toward lower NFC ($P < 0.05$) and higher LSI ($P < 0.01$) during the 1950 s and the 2010 s. In addition, BIO4 in the occurrences in 2010 s was higher than those in 1950 s, with marginal significance ($P = 0.06$). Furthermore, we documented a 61.2% decrease in niche hypervolume between eras (1950 s volume=488186.6, 1970 s volume=189458.5) with a centroid distance of 4721.8 and a Sørensen similarity of 0.024, indicating obvious niche shifting at this interval.

4. Discussion

Despite the growth in protected areas globally, poor outcomes yielded as conservation managers have been misjudging the marginal habitats where a species occurs as optimal simply because it has persisted there (Kerley et al., 2020). Affected by historical range contractions, refugee species are confined to suboptimal habitats, with consequences of decreased fitness and density, and severe conservation risks (Kerley et al., 2012). Similarly, Hainan gibbons have been confined to suboptimal habitats in the BNNR with as few as 7–8 individuals and depend on anomalous resources, which might be most likely the key threat that caused the stagnation of the population before 2008 (Chan et al., 2005; Jiang, 1996; Zhou, 2008) (also see Table S3 in Appendix 2 for details). Therefore, understanding historical population trends and quantifying the niche shifts of rare populations based on their historical occurrences are critically important for making the best efforts to preserve species (Bonebrake et al., 2010). Here, we constructed a dataset of historical occurrences of Hainan gibbons based on multiple sources and then estimated the effects of anthropogenic drivers on the shrinking distribution of this species.

We estimated the relative importance of anthropogenic drivers and other environmental variables based on the SDMs constructed using datasets from the 1950 s and 1970 s. Human disturbance ranked as the most important factor influencing the distribution of Hainan gibbons in the 1950 s, and as the third most important factor in the 1970 s, indicating that the distribution of this species on Hainan Island were primarily affected by human disturbance and habitat transformation. Habitat suitability was much more associated with LSI than NFC in the 1950 s but was more influenced by NFC in the 1970 s, which may have resulted from deforestation in this interval. Because the Hainan gibbon is an obligate tropical forest specialist, a lower NFC reduces the habitat suitability (Chan et al., 2005). The probability of gibbon presence decreased with an increase in the minimum temperature of the coldest month (BIO6), which may reflect the removal of gibbons from warmer areas (low elevations) in the past (Peng et al., 2008), rather than the biological

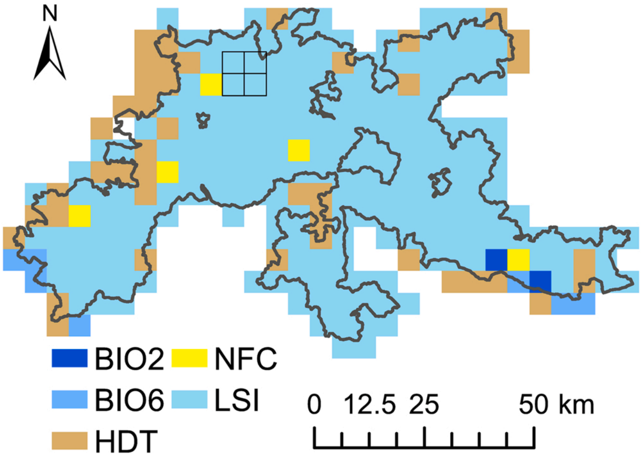

Fig. 4. Limiting factors for the presence of Hainan gibbon across Hainan tropical forest national park (HTFNP) in 2010 s predicted by the MaxEnt using 1950 s data. The black squares indicate the occurrence grids of this species in the current period (2020 s), and the grey line indicates the boundary of HTFNP. BIO2, BIO6, HDT, NFC, and LSI indicate mean diurnal range, minimum temperature of the coldest month, the level of human disturbance and habitat transformation, the natural forest cover, and the landscape shape index, respectively.

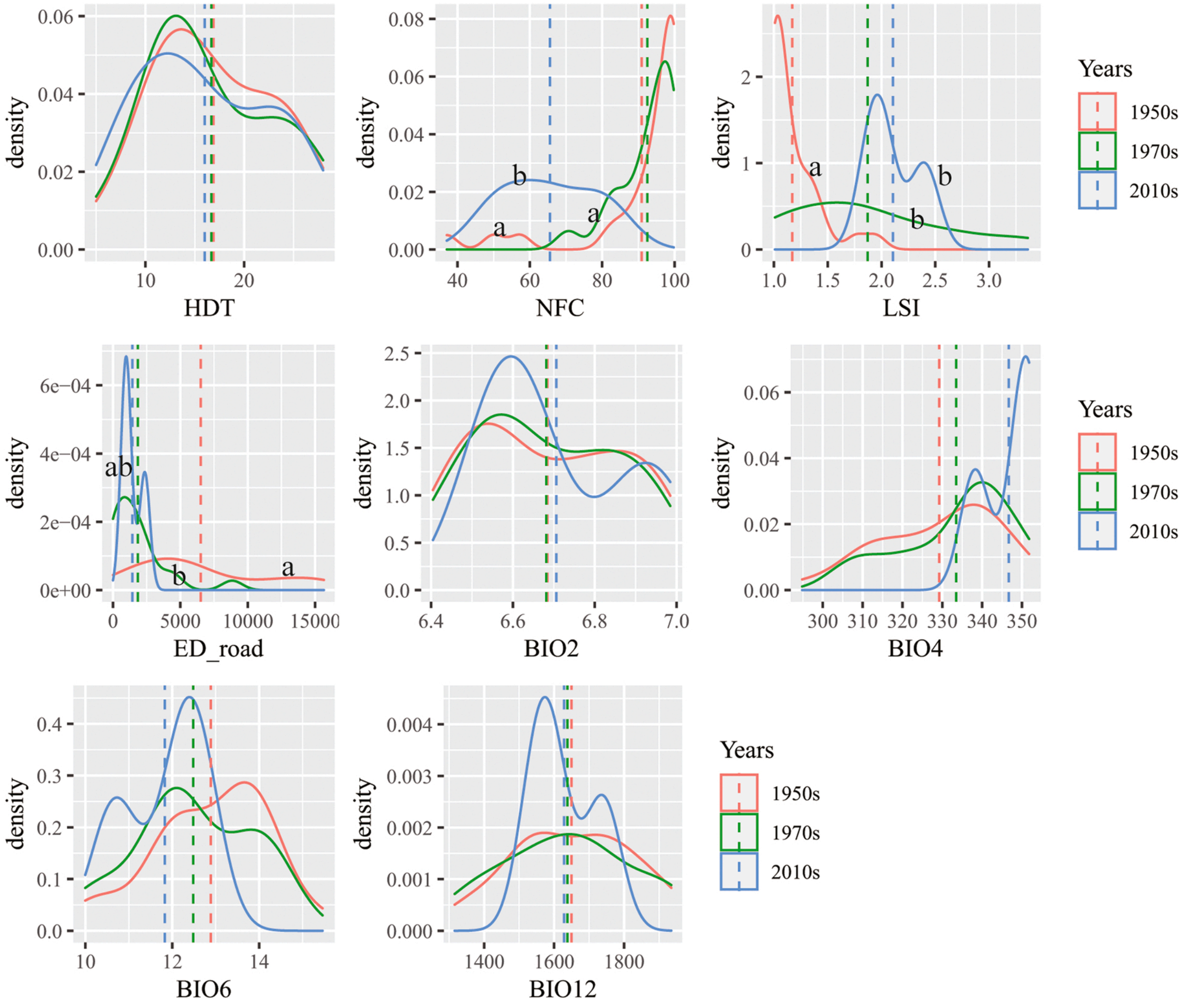

Fig. 5. Probability density curves of the environmental variables in Hainan gibbon occurrences during the 1950 s, 1970 s, and 2010 s, with HDT, NFC, LSI, ED_road, BIO2, BIO4, BIO6, and BIO12, which indicate the level of human disturbance and habitat transformation, the natural forest cover, the landscape shape index, the Euclidean distance to the nearest road, mean diurnal range, temperature seasonality (standard deviation ×100), minimum temperature of coldest month and annual precipitation, respectively. The dotted lines indicate the average value of the responding variable in different periods. Curves that do not share the same letter (a or b) were significantly ($P < 0.05$) different from each other, whereas those curves without letters were not significantly different from each other in terms of the same variable.

response of this species. Although previous studies have reported that precipitation influences the group size and biomass of primates (Bryant et al., 2015; Janson and Chapman, 1999), and the phenology of gibbon food species (Bach et al., 2017; Du et al., 2020), it showed a limited contribution to Hainan gibbon distribution in this study.

Our two SDMs (Models *a* and *b*) predicted that habitats would decrease during the 1950–2010 s. However, Model *a* predicted 167.9%, 109.7%, and 388.2% of the habitats predicted by Model *b* for the 1950 s, 1970 s, and 2010 s, respectively. The areas predicted by Model *a* may only indicate the ones most vulnerable to human disturbances but were not identified as suitable based on 1970 s data. This is because these recent occurrences represent only a subset of the species' historical range, leading to an underestimation of species niches, which in turn can misguide conservation efforts (Monsarrat et al., 2019; Pang et al., 2022). Zhang et al. (2010) reported a 35% loss of suitable habitat during the 1991–2008 period using vegetation maps generated from remote-sensing images. Our predicted habitat in the 2010 s using the 1950 s dataset predicted more habitats southeast of Hainan Island than the prime gibbon habitat in 2008, as described by Zhang et al. (2010). In addition, our predicted habitat in the 2010 s coincided with reserves that had the most recent unverified gibbon sightings dated from the post-2000 period (Turvey et al., 2017). Therefore, the predicted suitable habitats require conservation and further research.

Furthermore, our comparison of niche volumes showed shrinkage of the realised niche of the Hainan gibbon during the 1950–1970 s, whereas our probability density curves of the nine environmental variables in the three periods revealed niche shifting driven by anthropogenic factors during the 1950–2010 s period. Compared with the 1950 s, the occurrence of Hainan gibbons in the

2010 s dominated in areas with lower natural forest coverage ($P < 0.05$) but higher fragmentation ($P < 0.01$) and in those that were closer to roads ($P = 0.08$), as well as those with larger temperature seasonality ($P = 0.06$) and lower minimum temperature of the coldest month ($P = 0.19$). Thus, it is strongly suggested that the species' habitat requirements be assessed for future conservation management by compiling historical data on the target species, such as the Hainan gibbon.

However, the distribution of Hainan gibbons based on historical occurrence had reduced by 32.14% in the 1970 s and by 89.29% in the 2010 s compared with that in the 1950 s, which was much faster than the loss of suitable habitats predicted by SDM. This is partly due to the delayed effects of population extinction response to the decline of habitat quality, or "extinction debt" (Haddad et al., 2015; Tilman et al., 1994), and also confirmed the hypothesis that population in smaller or more isolated remnants are more likely to decline and become extinct (Bruna, 2004). In addition, the population showed an even sharper decline, in that > 95% of the population disappeared during the 1950–1970 s period (Jiang, 1996; Liu et al., 1984) (Appendix 2, Table S3), coinciding with our records of the distribution and intensity of gibbon harvests, indicating severe damage caused by targeted hunting during this period.

Hunting has historically been a livelihood for local people on Hainan, where gibbons were hunted for winemaking, traditional medicine, or bushmeat (Chan et al., 2005; Tang and Li, 1957; Yan, 2008). Before the implementation of the Natural Forest Conservation Program in 1998, hunting and logging were the two main threats to Hainan gibbons, although hunting is likely to cause greater threats to wildlife than deforestation (Redford, 1992; Sethi, 2022). Unfortunately, the effects of hunting may be amplified when the population is extremely small, as with the Hainan gibbon. For instance, the marked decline in the Hainan gibbon population (from 21 to 15 individuals) during the 1989–1993 period was caused by hunting and deforestation due to a lack of financial support for the proper management of nature reserves (Chan et al., 2005; Wang, 1995; Zhou et al., 2005). In addition, the sharp decline in the 2000–2003 period was suspected to be caused by hunting because deforestation had been stopped by 1995, even though this is difficult to validate (Bryant, 2014; Fellowes et al., 2008; Zhou et al., 2009).

Generally, anthropogenic drivers, such as land use, forest product collection, and logging, may cause an avoidance response in animals, resulting in a reduced probability of presence in areas near a disturbance (Johnson and Russell, 2014; Zhao et al., 2016). However, the environmental conditions of the harvested gibbons were not significantly different from those of gibbons from the 1950 s to the 1980 s. These results indicate that anthropogenic disturbances, including hunting, probably occurred across the distribution of the Hainan gibbon rather than just in some parts, which possibly explains why the population declined rapidly in the last century (Liu et al., 1984). However, illegal hunting is still common in the forest on Hainan Island and has been recorded recently (Turvey et al., 2017); and poaching of other wildlife with rifles and traps continues to occur within the BNNR; therefore, this species is still potentially threatened by hunting activity (e.g., accidental shooting through mistaken identity) (Geissmann and Bleisch, 2020; Liu et al., 2022). Conversely, Hainan gibbons occurred in two grids predicted to be unsuitable habitats in the 2010 s, which may be due to the conservation efforts in the BNNR, including hunting restrictions and forest protection (Zou et al., 2022). This could also suggest that currently unsuitable habitats, especially those adjacent to suitable habitats, are likely to be restored, assuming that serious conservation management would be conducted.

5. Conclusions and suggestions

Our research provides an approach to estimate the habitat requirements for endangered species with limited available occurrences. We simulated the habitat of the Hainan gibbon based on occurrences from multiple sources of historical gibbon records by correcting for sampling bias. Our model revealed that the distribution dynamics of Hainan gibbons since the 1950 s were primarily driven by anthropogenic factors, with the importance of the NFC increasing from the 1950 s to the 1970 s. The model constructed using 1950 s data identified a larger suitable habitat than the model based on 1970 s data, which highlights the critical importance of using historical occurrence data to reconstruct habitat requirements, especially for species that have suffered significant range contractions under human pressures. Only one grid of the 2010 s/2020 s occurrences was predicted to be a suitable habitat (only by the model using the 1950 s data), indicating a suboptimal habitat but conservation efforts on current occurrences. Therefore, conservation planning for Hainan gibbons should not only focus on existing habitats but also on the identification of more effective protected areas, such as those predicted by the model using the 1950 s data, as emphasised by Kerley et al. (2020).

We strongly recommend that:1) conservation efforts should pay more attention to the predicted suitable habitat, where the habitat structure and resource distribution should be studied to contribute to science-led forest restoration (Liu et al., 2020); 2) habitat recovery should be conducted to improve the quality of habitats, for example, by eliminating the limiting factors in the HTFNP, while constantly monitoring potential hunting in this area; and 3) potential corridors should be developed among isolated patches to provide climate refuges, considering that primates are vulnerable to threats from climate change (Dunham et al., 2011; Pacifici et al., 2017). As Hainan gibbons are able to utilise secondary forests and substantially expand their range (Chan et al., 2020), constructing corridors among habitat patches will benefit the dispersal of the population to potential habitats in the southern part of the BNNR.

CRediT authorship contribution statement

Haisheng Jiang, Yuke Zhang and Jiehua Yu contributed to the study conception and design. Data collection were performed by Jiehua Yu, Siliang Lin, Jiekun He, Yang Xu, Jiahao Tu and Haisheng Jiang; Data analysis by Yuke Zhang and Jiehua Yu. The manuscript was written by Yuke Zhang, and all authors read and approved the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

I have shared the link to my data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02472.

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