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Distribution range contractions and identification of conservation priority areas for canids in Sichuan Province, China

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ABSTRACT

Canids are among the numerous taxonomic groups that have recently experienced significant population declines. The reconstruction of distribution range changes using long-term ecological data can reveal processes underlying spatial contractions that short-term studies may not detect. We integrated ecological niche modeling with long-term ecological records to estimate the magnitude of canid range contractions in Sichuan Province over the last 50 years. Our findings indicate that canid distributions underwent sharp contractions between the 1970 s and 2010 s (contraction rates: gray wolf *Canis lupus* 24.62%, dhole *Cuon alpinus* 75.65%, red fox *Vulpes vulpes* 48.63%, Tibetan fox *V. ferrilata* 26.88%, and raccoon dog *Nyctereutes procyonoides* 30.84%). Concerning environmental variables, our results suggest that altitude, dd < 18 (degree-days below 18 °C, heating degree-days), LUCC (land use), and human population density contributed the most to patterns of canid distribution between the 1970s and 2010s. Canid contraction rates in nature reserves were significantly lower than in other types of protected and non-protected areas. For all study species, 47% of the canid conservation priority areas on average have been protected in Sichuan Province. The Chinese government has recently upgraded canid species' protection level and established more national parks. However, it is critical to invest in the surveillance of anthropogenic disturbance, compensation schemes for human–wildlife conflict, and public wildlife conservation education.

1. Introduction

Species distribution ranges are shrinking, shifting, and becoming fragmented as a result of global environmental changes (Chen et al., 2011). Land use change and climate change are considered to be the main drivers of species distribution changes (Bellard et al.,

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2012; Davison et al., 2021), causing nearly 27% of mammalian ranges to shift and contract (Schipper et al., 2008). The expansion and intensification of human land use and modification of natural habitats have caused a decline in global terrestrial biodiversity of more than one-fifth (Hill et al., 2018) and a 50% reduction in global vegetation biomass (Erb et al., 2018). Meanwhile, wild mammal biomass has declined by more than 75% (Bar-On and Milo, 2018). The balance between natural habitats and human-dominated landscapes determines species diversity and distribution (Goldewijk et al., 2015). On the one hand, unprecedented expansion of agriculture and industry has changed which land cover types predominate (Channell and Lomolino, 2000); on the other hand, increased outdoor recreation and agricultural activities have led to repeated human-wildlife encounters (Andrew et al., 2009), ultimately forcing animals to adjust their habitat selection criteria (Lima and Bednekoff, 1999) and causing species distributions to contract.

Sichuan Province has five species of canids: the gray wolf (*Canis lupus*), dhole (*Cuon alpinus*), red fox (*Vulpes vulpes*), Tibetan fox (*V. ferrilata*), and raccoon dog (*Nyctereutes procyonoides*). They were once widely distributed across 99 counties within Sichuan Province (Wang and Hu, 1999; www.iucnredlist.org). Although they belong to the same family, there are some differences in their ecological niches. First, in terms of habitat altitude, *V. ferrilata* lives at the highest altitudes, chiefly distributed in the Western Sichuan Plateau at an altitude of 3600–5200 m (Wang and Hu, 1999; Liu and Wu, 2019). *C. lupus* and *V. vulpes* inhabit the middle-high altitude zone (~2000–5000 m) outside of the East Sichuan Plain (Liu and Wu, 2019). *Cuon alpinus* lives at the boundary between the Alpine Valley and the East Sichuan Plain in the mid-altitude zone (1500–3500 m) (Liu and Wu, 2019; Li et al., 2020). Finally, *N. procyonoides* inhabits the Alpine Valley and Southern Sichuan Middle Mountains below 2000 m (Liu and Wu, 2019). Differences in altitude shape land use and climate types. With the exception of *V. ferrilata*, the other four canids used forest (Liu and Wu, 2019), and while shrubland was disfavored by *C. alpinus* and *V. ferrilata*, all five canids inhabit grasslands (Liu and Wu, 2019). Except for *N. procyonoides*, the other four canids also used bare land (Liu and Wu, 2019). In addition, *V. vulpes* can occasionally be found on cultivated lands and artificial surfaces, and *N. procyonoides* often inhabits wetlands (Liu and Wu, 2019).

Large carnivores such as canids occupy important trophic niches and play critical ecological roles in regulating the structure and dynamics of biological communities (Ford and Goheen, 2015). Therefore, canid range contractions and local extinctions can have major trophic consequences across ecological systems (Elmhagen et al., 2010; Wolf and Ripple, 2017; Srivathsa et al., 2020). Recent studies have shown that in Sichuan Province's Giant Panda National Park, *Canis lupus* have retreated to the Minshan and Qionglaishan ranges, while *Cuon alpinus* were only sporadically found in the Qionglaishan ranges (Li et al., 2020). Though the extent of the canids' range is rapidly deteriorating, impacted by habitat fragmentation (Xia et al., 2020) and anthropogenic factors (Iyengar et al., 2005) as well as retributive persecution owing to alleged livestock depredation (Gopi et al., 2012), these carnivores have not attracted sufficient attention from the Chinese government, in contrast with flagship species such as the giant panda (*Ailuropoda melanoleuca*) (Wei et al., 2019) and snub-nosed monkeys (*Rhinopithecus spp.*) (Li et al., 2002).

Species distribution models (SDM) can predict the potential distribution area of species by establishing the mathematical relationships between species location and environmental variables (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). SDM is now widely used to determine potential distribution (Clements et al., 2012), the effectiveness of conservation efforts (Kabir et al., 2017), biological invasions (Thuiller et al., 2005), and species reintroduction (Olsson and Rogers, 2010). Species distribution changes may occur over longer periods (Bellard et al., 2012), meaning short-term studies are sometimes inadequate to accurately assess these changes and their underlying mechanisms. Therefore, long-term trends should be investigated based on historical data. The emergence of numerous species databases has provided new opportunities to analyze species distribution and conservation (Jetz et al., 2012). However, species location records typically represent the species' geographic distribution only at a particular point in time (Rondinini et al., 2010) and cannot be extrapolated to areas that were not surveyed. The nature of such data also precludes inferences regarding the impact of environmental changes on a species' habitat over lengthy time scales (Hoegh-Guldberg et al., 2008). Therefore, SDM was used to predict the suitable distribution area (SDA) of canids within a specific period. This approach has been applied to Chinese pangolins (*Manis pentadactyla*) (Yang et al., 2018) and black-billed capercaillies (*Tetrao urogalloides*) (Zhuang et al., 2020), among other species.

Species conservation plans should be implemented based on foundational natural history information about the target species (Pimm et al., 2014), but conservationists often focus on a species' current status while overlooking the historical context in which its distribution changed. The reconstruction of range changes based on long-term ecological data can reveal the processes and factors underlying these changes (Yang et al., 2018). We chose Sichuan Province as the research area because of its stark variations in altitude (range: 191–6243 m) and unique climatic and geomorphology types. These particular geographic, climate, and vegetation profiles have contributed to Sichuan Province's status as a canid stronghold, with five of China's seven wild canid species occurring there (Liu and Wu, 2019). A focus on this province helps to highlight the impact of environmental factors such as climate, topography, land use, and human disturbance on the distribution of canids. Dynamic changes in distribution can reflect species' biogeographical characteristics (Guisan et al., 2013). This study aggregates canid distribution data from Sichuan Province over the last 50 years and uses a species distribution model to predict potential suitable canid habitats in each period. This model allowed us to examine the contraction in the range of these species within the same period. We also estimated the conservation effectiveness of five canid protection schemes and priority protected areas.

2. Materials and methods

2.1. Study area

Sichuan Province is located in the southwestern region (26.063–34.311°N, 97.351–108.549°E) of mainland China. It can be divided into five geographic units according to its topography: the Western Sichuan Plateau, Alpine Valley, Southwest Sichuan Platform, East Sichuan Plain, and Northern and Southern Sichuan Middle Mountains (Fig. 1).

2.2. Occurrence data

Following the data collection process described in previous research (Zhang et al., 2017; Yang et al., 2018), we collected canid data from nine sources: GBIF, local gazetteers, fauna records, scientific surveys of nature reserves, published scientific research, specimen records, field investigations, news, and interviews (Yang et al., 2018). A total of 266 documents were collected: 127 from local gazetteers, 4 from fauna records, 85 from nature reserve surveys, and 50 from published scientific research articles. After collecting data from historical documents, we searched the GBIF Database and the Chinese Terrestrial Vertebrate Database for canine distribution information as well as survey data from our infrared cameras (347) for the past decade. Finally, for areas not covered by the above methods, we interviewed 67 local forestry officials, 13 wildlife experts, and 150 knowledgeable residents of the community to supplement the species occurrence data (see details in Electronic Supplementary Material).

We extracted all location information from Google Earth. To prevent potential bias caused by clustered occurrences, we removed duplicate records according to the canids' "daily activity distance". Owing to a lack of unified daily activity distance information for the five canid species, we combined the relevant literature (Duan et al., 2016) and set the daily activity distance to 5 km; each 5 km × 5 km grid included only one occurrence point. Ultimately, we obtained 1031 occurrence data points for the 1970s (1970–1979), 978 for the 1980s (1980–1989), 848 for the 1990s (1990–1999), 522 for the 2000s (2000–2009), and 335 for the 2010 s (2010–2021) (Table 1).

2.3. Environmental variable database and variable selection

Four environmental variable types were used in this study: climate, topography, land use, and human population density. Climate change is thought to be one of the main drivers of distribution changes (Bellard et al., 2012; Davison et al., 2021). The suitability of a habitat for a species will change with climate change, especially as temperature and precipitation are affected (Sandel et al., 2011), causing mammalian ranges to shift and contract (Schipper et al., 2008). We included climatic conditions characterizing species distributions using a set of temperature and precipitation variables (ahm, cmd, dd<0, dd>5, dd<18, dd>18, emt, eref, ext, cmd, map, mcmt, mwmt, nffd, pas, td; size, 1 ×1 km; see details in Table S1) downloaded from Climate AP v. 2.03 (http://climateap.net/) (Wang et al., 2012). Topography (elevation, aspect, and slope) alters canids' thermal niche, thereby limiting survival and geographical distribution (Barton et al., 2019), so topography data were obtained from the SRTM 90 m Digital Elevation Database (http://srtm.csi.cgiar.org/; size, 0.25 km × 0.25 km). Finally, land use, such as the distribution of forest and grassland, and human disturbance represented by human population density will also affect the distribution of animals (Di Marco and Santini, 2015), especially for canids

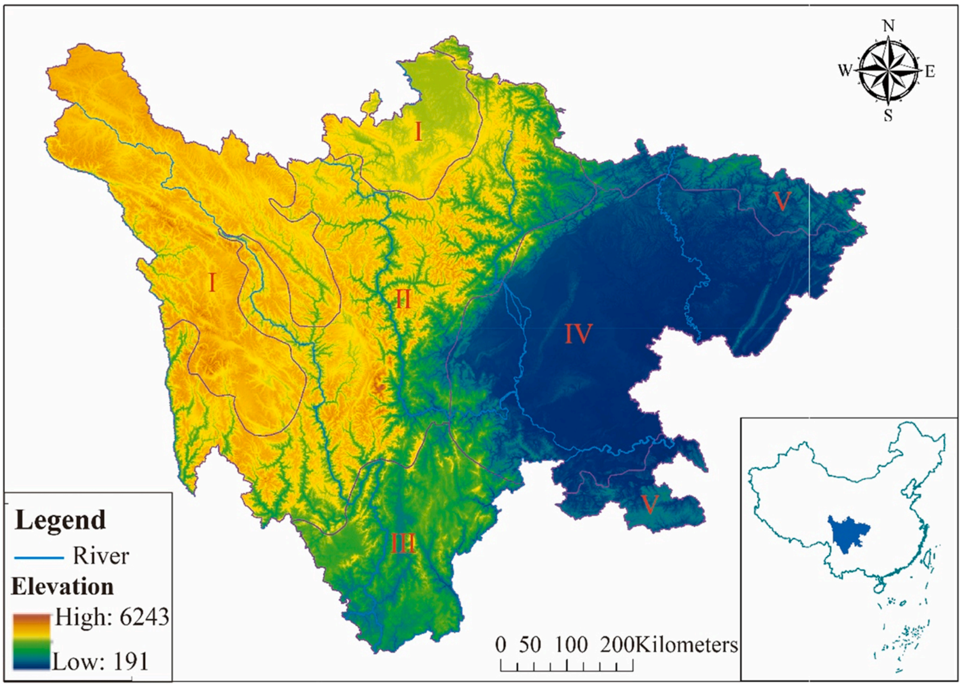

Fig. 1. Study area and five geographical units I, the Western Sichuan Plateau; II, Alpine Valley; III, Southwest Sichuan Platform; IV, East Sichuan Plain; V, Southern Sichuan Middle Mountain.

Table 1
Canids occurrence data and accuracy of species distribution range models in different periods.

Species	Period	Sources and number of occurrence data										AUC	Range (km^2)
		All	I	II	III	IV	V	VI	VII	VIII	IX		
Canis lupus	1970s	243	0	41	17	54	18	10	71	2	30	0.821	254,077
	1980s	235	0	38	17	54	18	8	68	2	30	0.817	202,606
	1990s	213	4	24	17	54	14	8	64	0	28	0.811	200,071
	2000s	109	5	0	0	51	9	2	17	0	25	0.831	193,770
	2010s	79	0	0	0	48	6	0	0	0	25	0.818	191,533
Cuon alpinus	1970s	190	5	51	28	34	20	3	2	2	45	0.81	168,907
	1980s	185	5	51	26	34	19	3	0	2	45	0.86	109,216
	1990s	165	5	48	17	32	15	3	0	0	45	0.866	74,917
	2000s	119	0	38	10	26	11	2	0	0	32	0.843	69,247
	2010s	57	0	0	0	22	5	2	0	0	28	0.871	41,132
Vulpes vulpes	1970s	342	21	51	28	55	34	6	97	5	45	0.837	251,908
	1980s	332	21	51	26	55	31	6	92	5	45	0.828	215,713
	1990s	253	21	48	17	45	15	6	81	5	15	0.835	148,097
	2000s	165	21	28	4	35	11	2	53	3	8	0.863	149,152
	2010s	112	21	0	0	32	5	0	46	0	8	0.865	129,393
Vulpes ferrilata	1970s	94	3	14	8	17	20	3	15	0	14	0.834	163,617
	1980s	77	3	9	5	15	15	3	15	0	12	0.857	142,397
	1990s	76	3	9	5	15	15	3	14	0	12	0.857	156,436
	2000s	61	0	7	5	14	11	2	13	0	9	0.814	151,717
	2010s	45	0	0	4	12	5	2	13	0	9	0.855	119,638
Nyctereutes procyonoides	1970s	92	3	12	8	15	20	3	9	0	22	0.891	126,175
	1980s	83	3	9	6	15	19	3	9	0	19	0.893	121,325
	1990s	74	3	9	6	15	16	3	4	0	18	0.889	111,861
	2000s	65	0	9	6	14	13	2	3	0	18	0.924	98,603
	2010s	42	0	0	4	11	5	2	3	0	17	0.919	87,258

Occurrence data Sources: I,GBIF; II, local gazetteers; III, fauna records; IV, scientific surveys of nature reserves; V, published scientific research; VI, specimen records; VII, field investigations; VIII, news; IX, interviews.

with strong transfer ability; these data were provided by the Geographical Information Monitoring Cloud Platform (http://www.dsac.cn/; size, 1 km × 1 km). A total of 21 variables were obtained for further analysis. We used ArcGIS 10.6 to resample these 21 variables to achieve a precision of 1 km × 1 km.

We used a pairwise diagnostic tool (variance inflation factor, VIF) to reduce collinearity among predictor variables and exclude highly correlated predictor variables (threshold = 10, VIF > 10 indicates variance over 10 times as large as a case of orthogonal predictors) (Dormann et al., 2013). VIF was calculated with R version 3.4.3 using the 'BiodiversityR' package. For each period, 8–11 variables were selected for modeling (see Table S3).

2.4. Model analysis method

MaxEnt is the most effective and widely used model in SDM (Phillips et al., 2006; Elith et al., 2006; Phillips and Dudík, 2008). Based on the maximum entropy theory, MaxEnt can predict the potential suitable distribution area of species utilizing information about the observed distribution of species (Phillips et al., 2006). MaxEnt provides several significant advantages in SDM, such as strong and comprehensible estimates with presence-only data alone (Merow et al., 2013; Phillips and Dudík, 2008). MaxEnt minimizes the two probability densities defined by covariate space (one estimated from the presence data, one estimated from the landscape), making it easier for many users to understand the modeling (Elith et al., 2011). At the same time, it permits integrating environmental variables with the geographical coordinates of species and constructing ecological niche maps to depict the suitability levels of species in different regions (Renner et al., 2015). In the case of insufficient sample breadth and complexity, reliable modeling performance can still be obtained (Elith et al., 2011). Given that we only collected presence data and that data were not extensive enough, we used MaxEnt 3.3.3k (Phillips et al., 2006) to estimate the potential distribution of canids in Sichuan Province over time.

Canid occurrence records and bioclimatic variables in each period were input separately into the model to predict potential canid distributions across different periods, and occurrence records were randomly divided into two groups: 80% were used to train the model, and 20% were used to validate it. Because we modeled multiple species, we employed default regularization and feature settings to maintain consistency (Tanner et al., 2016; Barber et al., 2022). 10,000 background points were used to estimate environmental change across the region of interest and to determine species' habitat preferences. Jackknife was used to assess variable contributions, and the model was replicated 10 times (Johnson et al., 2016). The area under the receiver operating characteristic (ROC) curve (AUC) and average omission error was used to evaluate model performance (Jiang et al., 2016), where greater AUC values indicated higher model prediction accuracy (Gonzalez et al., 2011). The maximum training sensitivity plus specificity (MaxSS) method was used to determine thresholds, and the average suitability (i.e., occurrence probability) of each grid was binarized to predict the final canid distribution (Liu et al., 2013).

2.5. Identification of conservation priority areas

We prioritized canid landscapes using the core-area zonation algorithm in Zonation 4.0.0 (C-BIG, Helsinki, Finland) (Moilanen et al., 2005; Moilanen, 2007). The algorithm iteratively removes the least valuable raster based on the MaxEnt result, and the contribution of the remaining output rasters to the species distribution is defined as the minimum aggregate loss of conservation value (Moilanen, 2007). As agricultural land, urban land, grassland, shrubland, and forested land can be critical to the canids, we selected these variables in the 2010 s as the condition layers (Yang et al., 2018). We further assume that the time of animal disappearance is correlated with a cost: the longer an animal is gone, the more difficult it is to recover the population, covering the SDM results for each period and converting them to cost layers (Yang et al., 2018). The algorithm creates a prioritization raster from 0 to 1 by identifying the core area, scaled according to the importance of species conservation (0 being the lowest priority and 1 being the highest) (Moilanen, 2007). We defined the top 10% of grids with the highest habitat quality as conservation priority areas for canids (Zhang et al., 2022).

2.6. Contraction rate, conservation priority areas in different types of protected areas

Protected area boundaries were obtained from the Sichuan Province Forestry Department. According to the definitions of the six protected area types, we divided them into two categories: nature reserves (i.e., strictly protected areas) and other protected area types (i.e., protected areas with science, education, and tourism functions including world heritage, forest park, scenic and historical areas, geoparks, and water parks). We overlaid the potential suitable habitats calculated by MaxEnt and the protection priority areas calculated by Zonation on the Sichuan protected areas layer to extract potential suitable habitats and protection priority areas in different types of protected areas. Paired sample T-tests were used to compare the range contraction rates within different types of protected areas.

3. Results

3.1. Model evaluation and main influencing factors in each period

Based on available records for canids at different periods in our study (Table 1), the ROC curves produced by the MaxEnt model showed that the average of 10 AUC test values for the five canid species, for different periods, exceeded 0.8 (all AUC values > 0.8; detAUC results for each period are shown in Table 1 and Fig. S1).

Relative contributions of the environmental variables were estimated, and the results indicated that variables affected the distribution of the five canid species differently (Table S3). Out of all the environmental variables, altitude, dd < 18, LUCC, and human population density made the largest contributions to canid distribution.

3.2. Contractions of potential distribution areas of canids in Sichuan Province from the 1970s to 2010s

Our results demonstrate that *Canis lupus* (254,077 km^2), *Cuon alpinus* (168,907 km^2), and *Vulpes vulpes* (251,908 km^2) were widely distributed throughout Sichuan Province during the 1970 s, particularly in the Alpine Valley. The potential distribution areas of *C. lupus*, *C. alpinus*, and *V. vulpes* in the 1970 s covered 38.72%, 25.74%, and 38.39% of the provincial area, respectively. During the 1970s, *V. ferrilata* was mainly distributed within the Western Sichuan Plateau as well as other alpine and canyon regions (163,617 km^2), and the potential distribution area covered 24.93% of the provincial area. *N. procyonoides* was mainly distributed in the Southwest Sichuan Platform Unit, the East Sichuan Plain, and the Sichuan Southern Middle Mountains (126,175 km^2); the potential distribution area covered 19.23% of the provincial area.

Over the past 50 years, the distribution of canids in Sichuan Province has markedly decreased. Suitable habitat area for *C. lupus* has decreased by 62,544 km^2 (total loss = 24.62%), with an average contraction rate of 6.45% per decade (20.26% between the 1970s and 1980s; 1.25% between the 1980s and 1990s; 3.15% between the 1990s and 2000s; and 1.15% between the 2000s and 2010s). *C. alpinus*' habitat in Sichuan Province has almost disappeared (total loss = 75.65%). To date, 127,775 km^2 of suitable habitat has been lost, and only 41,132 km^2 remains. The average contraction rate of *C. alpinus* was 28.73% per decade (35.34% between the 1970s and 1980s; 31.40% between the 1980s and 1990s; 7.57% between the 1990s and 2000s; and 40.60% between the 2000s and 2010s). *V. vulpes* was formerly the most widely distributed canid in Sichuan Province (251,908 km^2 in the 1970s), but the area of suitable habitat has declined by 122,515 km^2 (total loss = 48.63%) over the past 50 years, with an average contraction rate of 14.56% per decade (14.37% between the 1970s and 1980s; 31.35% between the 1980s and 1990 s; −0.71% between the 1990s and 2000s; and 13.25% between the 2000s and 2010s). *V. ferrilata* was mainly distributed in the plateau (163,617 km^2 in the 1970s), and the area of suitable habitat decreased by 43,979 km^2 (26.88%) over the past 50 years, with an average contraction rate of 6.82% per decade (12.97% between the 1970s and 1980s, −9.86% between the 1980s and 1990s, 3.02% between the 1990s and 2000s, 21.14% between the 2000s and 2010s). Finally, *N. procyonoides* has mainly been distributed in the plains, platform, and middle mountain regions (126,175 km^2 in the 1970s). Over the last 50 years, suitable habitat declined by 38,917 km^2 (total loss = 30.84%), with an average contraction rate of 8.75% per decade (3.84% between the 1970s and 1980s; 7.80% between the 1980s and 1990s; 11.85% between the 1990s and 2000s; and 11.51% between the 2000s and 2010s) (Fig. 2).

3.3. Canid contraction rates in different types of protected areas

We compared canid contraction rates among different types of protected areas (nature reserves vs. other protected areas and non-protected areas) and found that the contraction rate in nature reserves (mean contraction rate = 7.931%) was significantly lower than in non-protected areas (mean contraction rate = 15.898%, paired sample T-test , $t = 3.713$, $p < 0.001$), but there was no significant difference observed between nature reserves and other types of protected areas (mean contraction rate = 7.931%; paired sample T-test , $t = 0.935$, $p = 0.361$). Likewise, other protected areas and non-protected areas were not significantly different (paired sample T-test, $t = 1.958$, $p = 0.065$) (Fig. 3).

3.4. Evaluation of habitat protection and identification of conservation priority areas for canids

The established 112,163.74 km^2 of nature reserves and 60,204.93 km^2 of other protected area types were overlaid with currently suitable canid habitats, and the results revealed that the average proportion of suitable canid habitats within established protected areas in Sichuan Province is 47% (Table 2 shows the area and proportion of suitable habitats for the five canids in various protected areas).

The results of the core-area zonation algorithm showed that the conservation priority areas (CPAs) in protected areas of canid species were 18,364–39,076 km^2 (see Table 2 for the area of each species), and there was little overlap in the spatial distribution of

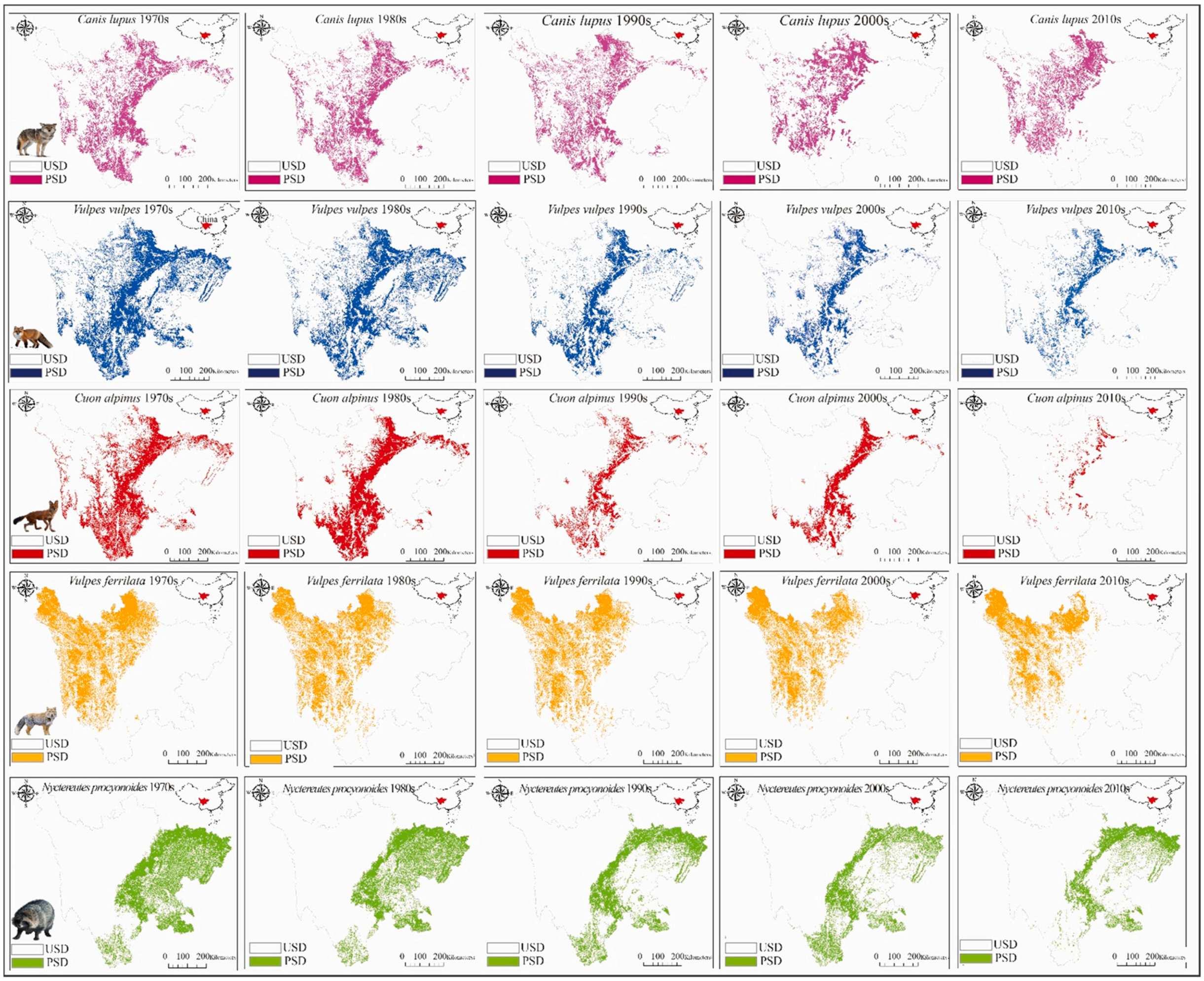

Fig. 2. Contraction of potential distribution areas of five canid species in Sichuan Province from the 1970–2010s USD, Unsuitable distribution; PSD, Potential suitable distribution. PSD of *Canis lupus*, PSD of *Vulpes vulpes*, PSD of *Cuon alpinus*, PSD of *Vulpes ferrilata*, PSD of *Nyctereutes procyonoides*.

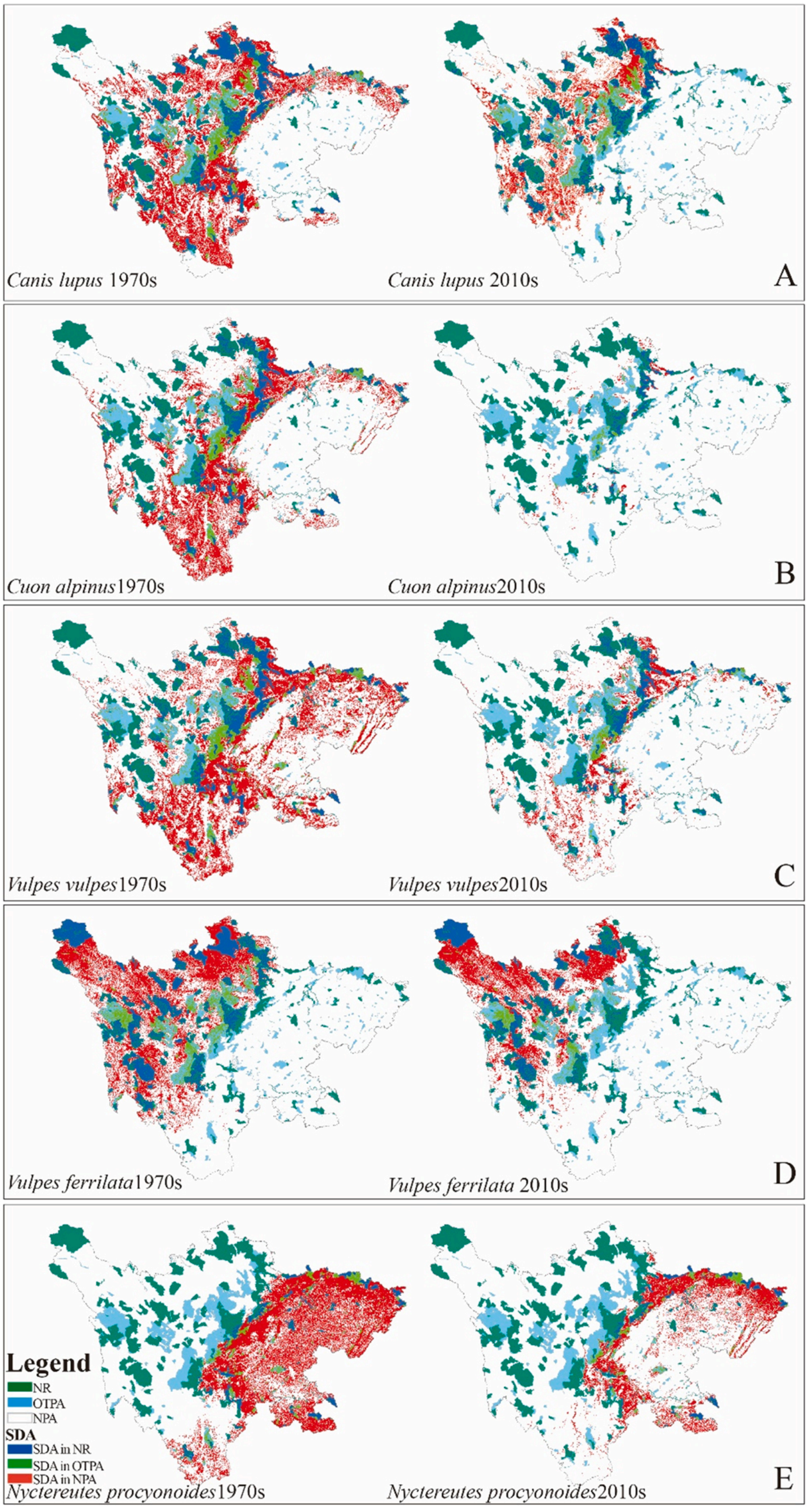

Fig. 3. Contraction of potential distribution areas of five canid species in different protected area types. NR, nature reserve; OTPA, other types of protected areas; NPA, non-protected areas; SDA, Suitable distribution area.

CPAs for canids (Fig. 4). Notably, nearly half (40.64–72.13%) of the CPA has not yet been incorporated into protected areas. As a non-endangered species that is not considered rare, 72.13% of the CPA of *N. procyonoides* is currently unprotected (see Table 2 for the proportion of each species' potential suitable habitat area that is protected).

Table 2
Area and proportion of suitable habitats for the five canids in types of protected areas.

Species	Areas of PA (km^2)			Areas of NPA (km^2)
	All		NR	OTPA
Canis lupus	39,076(59.36%)	25,800(39.19%)	13,276(20.17%)	26,756(40.64%)
Cuon alpinus	37,557(57.05%)	25,181(38.25%)	12,376(18.80%)	28,275(42.95%)
Vulpes vulpes	34,915(53.04%)	23,784(36.13%)	11,131(16.91%)	30,917(46.96%)
Vulpes ferrilata	24,794(37.66%)	22,677(34.45%)	2117(3.22%)	41,038(62.34%)
Nyctereutes procyonoides	18,364(27.90%)	10,806(16.41%)	7558(11.48%)	47,483(72.13%)

NR, nature reserve; OTPA, other types of protected areas; NPA, non-protected areas.

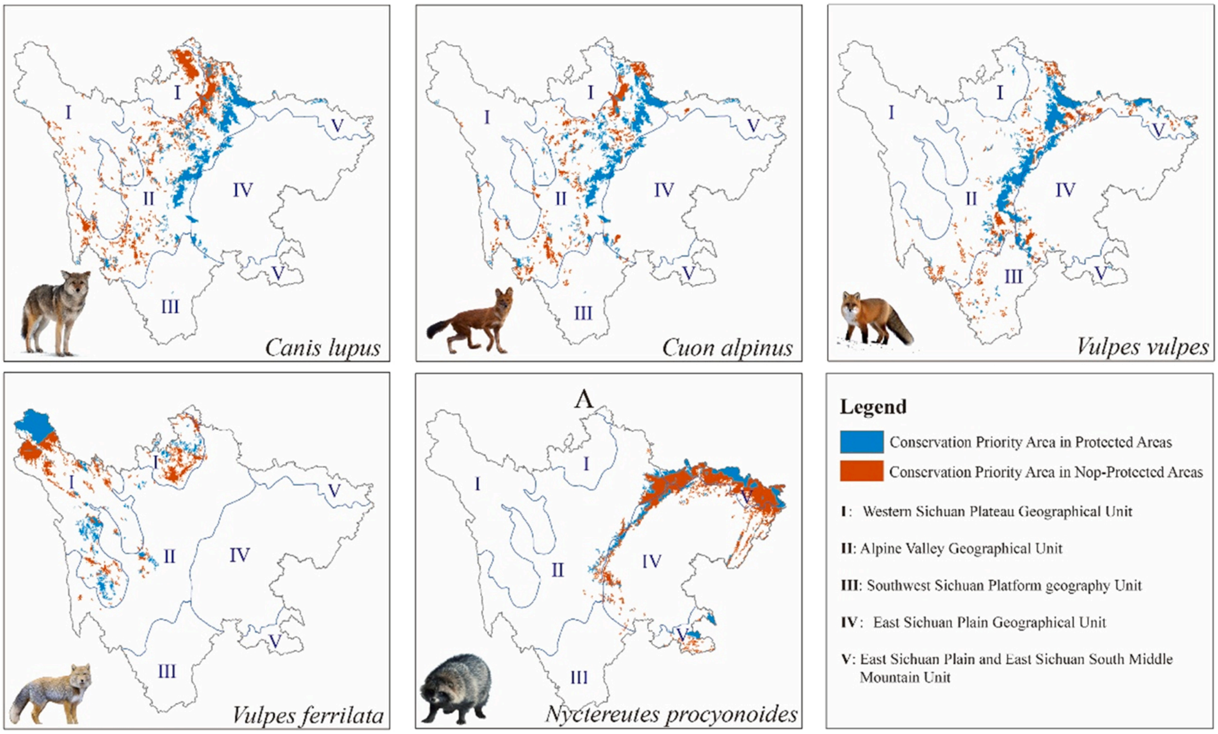

Fig. 4. Spatial distribution of conservation priority areas for five canids. Conservation priority area in protected areas (nature reserve and other types of protected areas) for five canids; Conservation priority area in non-protected areas for five canids Roman numerals represent different geographic regions.

4. Discussion

The suitability of any given habitat for mammals varies with environmental changes (Brodie, 2016). Our results suggest that altitude, dd < 18, LUCC, and human density had the greatest effects on canid distribution between the 1970s and 2010s. Extreme environments can play an important role in niche changes (Sexton et al., 2017). Specifically, warming temperatures cause canid distribution ranges to shift (Reshamwala et al., 2022). Higher human population density results in frequent human-canid conflict (Kabir et al., 2017; Lyngdoh et al., 2020), forcing canids to adjust their habitat selection criteria to avoid human disturbance (Lima and Bednekoff, 1999). Over the course of the period under study, the East Sichuan Plain, with its dense human population and low altitude, became unsuitable for canids. By contrast, the Alpine Valley, with its varied altitude and land use types (mostly forests and bare land) and sparse human population, will remain a high-quality habitat for canids in Sichuan Province (except *N. procyonoides,* which has special climatic requirements). This result is consistent with the forecasted future distribution changes of *Canis lupus* in Central Asia. Due to the comprehensive influence of rising temperatures and agricultural expansion, suitable habitat for *Canis lupus* will shift away from forests and incorporate more bare land (Brodie, 2016; Reshamwala et al., 2022).

Canids were once widely distributed throughout Sichuan Province (Jenks et al., 2012; Wang et al., 2016). Our results indicate considerable shrinkage in the canid suitable distribution area (SDA) over the last 50 years, particularly for *C. alpinus*, which shows a total loss rate of 75.65%. Species worldwide are currently undergoing rapid range shifts (Chen et al., 2011; Dirzo et al., 2014; Pimm et al., 2014), so it is unsurprising that canid ranges are contracting. However, our results contradict the hypothesis that in the future, the suitable habitat area for *Canis lupus* will expand in Central Asia (Reshamwala et al., 2022). Habitat contractions are primarily affected by climate change and anthropogenic disturbances including human encroachment and habitat modification (Bellard et al., 2012; Yang et al., 2018, 2020; Davison et al., 2021). Animals such as canids with strong migration ability can move to higher elevations (Walther et al., 2002; Root et al., 2003; Urban et al., 2013), even taking refuge on cultivated land and artificial surfaces during less favorable climatic conditions (Reshamwala et al., 2022).

We identify four main reasons for the contractions of suitable distribution area for canids in Sichuan Province over the past 50 years. First, although climate change affects species distribution, relatively mild and short-term climate change is not enough to transform ice sheets into grasslands or bare land for canids to exploit. Second, the "return farmland to forests or grassland" policy has not added much suitable habitat for canids. In the past 50 years, forested areas increased by 89,637 km^2 while grasslands decreased by 25,414 km^2, agricultural land retreated by 9203 km^2, and shrubland decreased by 53,209 km^2. Third, in the past 50 years, Sichuan's population has increased to 83.71 million, with a growth rate of 27.7%, overloading the landscape with human disturbance. The people are mainly concentrated in the central, eastern, and southern regions where the climate is suitable and altitude is lower (Fig. 1). Carnivorous canids will hunt livestock and even injure humans, and such "harmful animals" are often deliberately driven away (Gopi et al., 2012). This makes high-population density areas in central, eastern and southern Sichuan unsuitable as habitat. Meanwhile, the rapid development of tourism in recent decades has expanded the scope of human activities even in wilderness areas (Sanderson, 2002), further encroaching on canids. This has manifested through both increased tourist numbers and the construction of new tourist sites within formerly suitable canid habitat. Finally, although we did not evaluate diet and prey distribution and richness, both have a crucial impact on canid distribution (Hayward et al., 2015). As part of a general trend of animal range contraction (Chen et al., 2011; Dirzo et al., 2014), the reduced availability of suitable prey also limits canid distribution. The canids' contractions, it seems, has given their prey a better survival chance, but it has also allowed more adaptable animals, such as wild boars (*Sus scrofa*), to overrun the study area.

Our results revealed that the type of protected area matters with respect to the effectiveness of canid conservation. The canid contraction rate in nature reserves was significantly lower than in other protected and non-protected areas, similar to the situation of giant pandas (Zhuang et al., 2020). Nature reserves showed the strongest conservation effects among all protected area types and represent China's most important and longstanding biodiversity conservation spaces (Xu et al., 2008, 2014). Other protected area types (e.g., world heritage sites, forest parks, scenic and historical areas, geoparks, and water parks) are not specifically intended to conserve rare and endangered wildlife but rather are designed to facilitate tourism, entertainment, leisure, vacations, culture, education, and other activities. Such intensive human occupation may diminish the conservation utility of protected areas other than nature reserves.

Our study area encompassed 1,112,163.74 km^2 of nature reserves and 60,204.93 km^2 of other protected area types. At present, the average protected area coverage in Sichuan Province for all canid priority-protected areas is 47%. While this appears encouraging at first glance, results for each individual species indicate that the protection of non-endangered species (e.g., *N. procyonoides*) is considerably lower than that of rare and endangered species such as *C. alpinus*. Given the Chinese government's recent move toward increasing the protection level for canids, this situation may improve. For example, in 1989, the Chinese government listed *C. alpinus* as a "second-level" protected animal nationwide, while in the newly-revised "List of National Key Protected Wild Animals", *C. alpinus* was upgraded to a first-level animal, while *C. lupus*, *V. vulpes*, *V. ferrilata,* and *N. procyonoides* were listed as second-level (http://www.gov.cn/xinwen/2021-02/05/content_5585126.htm). The Chinese government has also begun promoting the construction of national parks with the aim of protecting large swaths of natural or near-natural areas as a means of conserving ecological processes and their associated species and ecosystem features (Ma, 2014). A further goal is to integrate and optimize nature reserves to resolve the incongruity between the spatial distribution of protected areas and the distribution of biodiversity (Zhang et al., 2022). However, several issues still require governmental attention. The contraction of wildlife distribution areas and restriction of animal activity due to human disturbance has become a global problem (Gaynor et al., 2018), and human population density in suitable canid distribution areas is very low. Therefore, the government is advised to pay attention to increasing human disturbance caused by the development of tourism and related infrastructure in recent years. Retributive persecution associated with livestock depredation and canid attacks on humans (Gopi et al., 2012) suggests that the government must balance tourism and economic development against wildlife protection, as well as increase compensation for wildlife accidents.

5. Conclusions

In this study, we reconstructed changes in canid distribution ranges in Sichuan Province using historical data from the 1970s to the 2010s. Our findings revealed that the area of suitable habitat for the five canid species we investigated contracted sharply within the last 50 years. The contraction rate in nature reserves was significantly lower than in other protected and non-protected areas. At present, the average protected area coverage rate in Sichuan Province for all canid conservation priority areas is 47%. The Chinese government has enhanced canid protection by establishing national parks and upgrading protected areas. However, it is still necessary to monitor anthropogenic disturbance (including tourism and its related infrastructure), increase compensation for incidents of human–wildlife conflict, and educate the public about the importance of wildlife conservation.

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CRediT authorship contribution statement

Wancai Xia: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **Cyril C. Grueter:** Writing – review & editing. **Chao Zhang:** Methodology, Software. **Hongfei Zhuang:** Methodology, Software. **Jie Hu:** Resources, Data curation. **Ali Krzton:** Writing – review & editing. **Dayong Li:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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

The data that has been used is confidential.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02499.

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