



Research Article

Predicting the effect of interspecific competition on habitat suitability for the endangered African wild dog under future climate and land cover changes

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Abstract

Apex predators play an important role in regulating ecological interactions, and therefore their loss can affect biodiversity across trophic levels. Large carnivores have experienced substantial population and range declines across Africa, and future climate change is likely to amplify these threats. Hence it is important to understand how future environmental changes will affect their long-term habitat suitability and population persistence. This study aims to identify the factors limiting the distribution of the endangered African wild dog, *Lycaon pictus*, and determine how biotic interactions and changing climate and land cover will affect future range suitability. We use Species Distribution Models (SDMs) to predict the current and future distribution of suitable conditions for *L. pictus* and its dominant competitor *Panthera leo*. We show that range suitability for *L. pictus* is limited by climatic and land cover variables, as well as high niche and range overlap with *P. leo*. Although both species are predicted to experience range contractions under future climate change, *L. pictus* may benefit from release from the effect of interspecific competition in eastern and central parts of its range. Our study highlights the importance of including land cover variables with corresponding future projections and incorporating the effects of competing species when predicting the future distribution of species whose ranges are not solely limited by climate. We conclude that SDMs can help identify priority areas for the long-term conservation of large carnivores, and therefore should be used to inform adaptive conservation management in face of future climate change.

Introduction

Climate change is recognised as the greatest impending threat to biodiversity across biomes (Millennium Ecosystem Assessment, 2005), and therefore predicting its impacts on species is a top conservation priority (Thuiller et al., 2008). Global trends in hydrology indicate that some regions, like Southern Africa, are expected to suffer critical water stress under future climate change due to increased frequency of extreme conditions, such as floods and droughts (Dallas and Rivers-Moore, 2014). Global temperatures have increased by $0.74 \pm 0.2^\circ\text{C}$ in the past 100 years, and are predicted to further rise by $2.0\text{--}4.5^\circ\text{C}$ by the end of this century, leading to the expansion and contraction of climatic zones and shifts in species' ranges (Langer et al., 2013).

Apex predators play an important role in regulating ecological interactions, maintaining ecosystem health and influencing lower trophic levels (Bruno and Cardinale, 2008; Schmitz et al., 2010). Their removal or disappearance can result in a loss of biodiversity and species richness across the ecosystem (Abade et al., 2014b). African wild dogs, *Lycaon pictus*, have been present in Africa since the Plio-Pleistocene, with fossil records dating back 2–3 million years in sub-Saharan Africa. At present, the population of free-ranging *L. pictus* is estimated at less than 8000 individuals and the species is classified as Endangered by the IUCN (Woodroffe and Sillero-Zubiri, 2012). Human population expansion, prey availability and interspecific competition are thought

to be some of the main factors limiting the areas which the species can safely inhabit. *L. pictus* has large home ranges ($150\text{--}2000\text{ km}^2$, depending on habitat) and is thought to use a variety of habitats, including woodland, bushy savannah, semi-desert, and short-grass plains (Kingdon and Hoffman, 2013).

Because *L. pictus* naturally occurs at low densities over vast ranges, habitat loss and fragmentation are major threats to its survival (Woodroffe and Ginsberg, 1999). Large carnivore habitat has been reduced dramatically across the African savannah, with some areas experiencing losses of over 75% (Watson et al., 2015). Many of the existing national parks and reserves may not be large enough to support viable populations of *L. pictus*. Reserves smaller than 10000 km^2 introduce edge effects (Woodroffe and Ginsberg, 1999) and packs can move beyond the boundary of reserves into human populated areas (Van Der Meer et al., 2011), increasing the incidence of human-wildlife conflict. Hence it is important to understand the anthropogenic and ecological factors influencing habitat suitability and range preferences of African carnivores in general (Kolowski and Holekamp, 2009), and in particular species like *L. pictus* that are becoming increasingly endangered and in need of guided conservation efforts. Future climate change is likely to amplify threats to *L. pictus* due to habitat fragmentation, further enhancing the importance of understanding the factors limiting the species range and identifying important areas for future conservation efforts (Watson et al., 2015).

L. pictus is one of five top carnivore species in Africa. Because of its smaller size it is likely to be outcompeted by the others, meaning that interspecific competition is a severe fitness-limiting factor for this species

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(Jackson et al., 2014). It often coexists with two other large carnivores: lions, *Panthera leo*, and spotted hyena, *Crocuta crocuta*. Although *L. pictus* typically has a higher hunting success than its competitors, individuals cannot defend themselves against attack. Therefore, they are at high risk of kleptoparasitism by larger carnivores, whereby the greater size (either body size or pack size) of the competitor will force *L. pictus* away from their fresh kill, resulting in a reduction in net energy gain (Van Der Meer et al., 2011). *L. pictus* do not typically avoid *C. crocuta*, either temporally or spatially, because their pack size is normally large enough to defend kills to prevent kleptoparasitism (Darnell et al., 2014). However, *L. pictus* are thought to avoid areas with high *P. leo* density, even if this requires inhabiting areas with reduced prey density (Van Der Meer et al., 2011). *P. leo* are responsible for as much as 12% of adult *L. pictus* mortality and 31% of pup mortality through direct attacks (Jackson et al., 2014). As such, interspecific competition with *P. leo* is likely to have a substantial effect on the ranging behaviour and habitat use of *L. pictus*.

Species Distribution Models (SDMs) offer an insight into the potential geographic distribution of species, from a local to global perspective (Peterson et al., 2014). Knowing the distribution, spatial arrangement and characteristics of environmental variables determining range suitability is essential for the conservation management of species (Brambilla et al., 2009). The main objective of SDMs is to gain an understanding of the factors underlying ecological patterns, which in turn allows for accurate predictions of future distributions (Miller, 2012). These models can help identify previously unknown environmentally suitable areas for the species and guide survey efforts to discover new populations (Brambilla et al., 2009). Applying SDMs in a predictive manner to model the effects of climate change can give an indication of extinction vulnerability, changes to range size and distribution shifts. Specifically, SDMs can help guide species long-term conservation efforts through identifying future suitable areas and predicting loss of current habitats (Schwartz, 2012).

Because species' ranges are rarely at equilibrium with climate, SDMs should incorporate other variables. Biotic interactions, such as interspecific competition, are important for identifying the realised niche of a species, i.e. the niche a species actually occupies as opposed to the niche it can theoretically occupy (Gillson et al., 2013). Incorporating interspecific competition from dominant species can improve the statistical modelling of species distributions (Austin, 2002). The role of biotic interactions was once thought to only shape species distributions at local spatial scales, but it is now recognised that these interactions have left their mark on the distribution of species from local to global scales (Wisiz et al., 2013). Recent studies have expressed the need for interspecific competition to be addressed when studying the range of carnivores (Van Der Meer et al., 2011; Vanak et al., 2013).

This study aims to understand the factors limiting the distribution and habitat suitability for the endangered African wild dog. We use SDMs to identify the environmental variables that are the principal predictors of *L. pictus* occurrence, and to predict how future climate and land cover changes can affect the species' distribution and long-term viability. SDMs are also constructed for *P. leo* to quantify the extent of range and niche overlap with *L. pictus*. We hypothesised that niche overlap between species will be relatively high as both species are carnivores with similar diets, and are therefore expected to preferentially occupy the same prey-dense areas. Therefore the predicted fundamental niche (the niche a species can occupy without the constraints of biotic interactions) will likely be different from the realised niche of *L. pictus* due to the effect of interspecific competition and competitive exclusion. We aim to highlight areas that will remain suitable for *L. pictus* with changing climate and land cover, and thus can be the primary focus of future conservation efforts for this endangered species.

Materials and methods

The potential distributions of the two study species, *L. pictus* and *P. leo*, were modelled under current and future conditions using the presence-only species distribution modelling approach Maxent (Phillips et al.,

2006). Maxent was consistently found to out-perform other modelling methods, in terms of higher Area Under the Receiver Operator Curve (AUC) scores (Khatchikian et al., 2010), better predictive ability (Elith et al., 2006) and not over-fitting suitable ranges (Peterson et al., 2007).

Location Records

Location records were downloaded from Global Biodiversity Information Facility (GBIF, www.gbif.org) for the two species, and were supplemented with records from published papers (Celesia et al., 2010; Githiru et al., 2014; Malcolm and Sillero-Zubiri, 2001; Peterson et al., 2014) and from direct observations by researchers. We excluded records older than 1970 and any records with inaccurate coordinates to ensure the best representation of current distributions within the study area. Biodiversity databases like GBIF are often criticised for being spatially biased due to unequal sampling efforts or record submission among countries and geographical areas. Such bias can distort our view of large-scale biodiversity patterns (Beck et al., 2014). Because spatial autocorrelation and surplus records can result in imprecise models and poor quality outputs (Miller, 2012) we used the nearest neighbour analysis in ArcGIS v10 (ESRI) to remove spatially clustered records. Maxent requires an unbiased dataset, and while many records were removed during nearest neighbour analysis, spatial sampling bias often cannot be avoided due to the location of research centres and studies (Brown, 2014). To counteract spatial biases and poor range representation due to the low number of available location records (*L. pictus* N=38, *P. leo* N=61), we generated bias layers to reflect uneven sampling efforts across the species' potential ranges. In ArcGIS we traced crude polygons containing 100 km buffer around clusters of location records

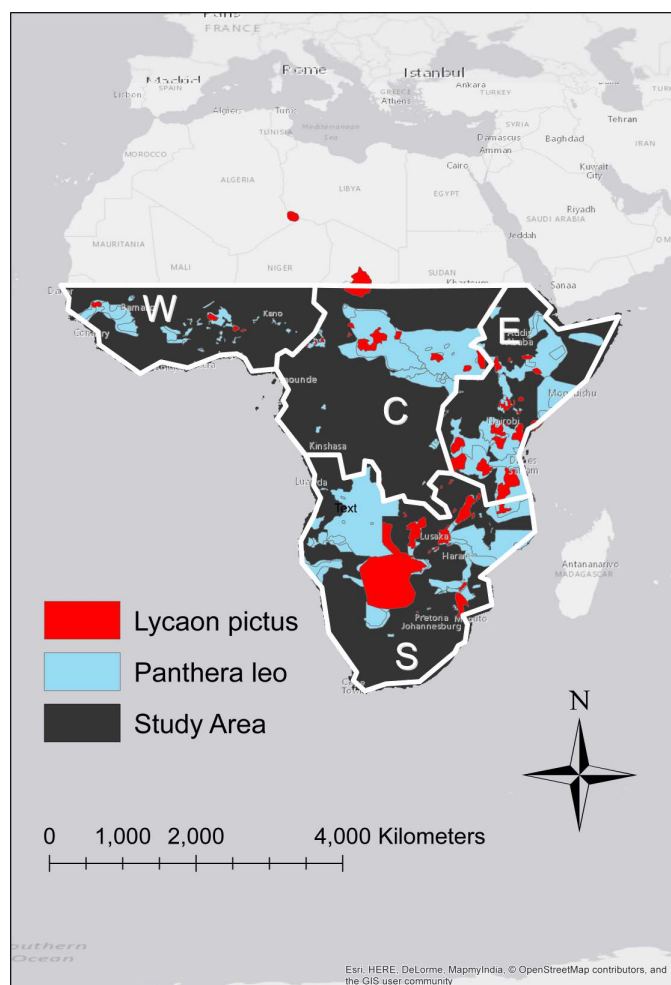


Figure 1 – The selected study area (in black) and species known ranges based on the IUCN RedList (Woodroffe and Sillero-Zubiri, 2012), displayed over an OpenStreetMap base map (ESRI). The geographical regions referred to in the manuscript are marked in white (W=West, C=Central, E=East, S=Southern Africa).

Table 1 – Environmental layers included in each of the species distribution models (Full = full model; Climate = climatic variables and IMAGE3 land cover variables; Full+Competitor = Full model plus competitor) for both species with the corresponding percent contribution, along with the average AUC test and train values. The climate models only incorporate the layers from the full models which have corresponding future projections. The *L. pictus* model with competitor includes all the layers from the *L. pictus* full model with the addition of the continuous output maps from the *P. leo* full model.

Environmental Layers	<i>Lycaon pictus</i>			<i>Panthera leo</i>	
	Full	Full+Competitor	Climate	Full	Climate
Temperature annual range (Bio7)	-	-	-	4.2	0.5
Mean temperature of coldest quarter (Bio11)	18.7	13.3	22.3	3.4	8.5
Annual precipitation (Bio12)	-	-	-	8.2	19.6
Precipitation of driest month (Bio14)	8.0	9.2	30.6	-	-
Precipitation of wettest quarter (Bio16)	9.7	8.1	14.1	-	-
Precipitation of warmest quarter (Bio18)	1.6	2.4	0.3	2.2	9.3
Precipitation of coldest quarter (Bio19)	0.5	0.8	0.7	-	-
Distance to barren lands	17.5	17.6	-	11.3	-
Distance to conifer woodlands	12.8	10.2	-	4.3	-
Distance to grasslands	3.0	3.5	-	8.2	-
Distance to karsts	9.1	7.1	11.5	2.5	6.7
Distance to urban areas	9.2	6.9	-	5.6	-
Distance to waterbodies	-	-	-	14.8	-
IMAGE3 land cover	9.8	6.8	20.4	26.2	55.3
Slope	-	-	-	8.9	-
Lion habitat suitability	-	14.1	-	-	-
AUC test	0.809	0.817	0.795	0.770	0.723
AUC train	0.884	0.900	0.842	0.865	0.786

within the same country to represent areas that are likely to have been sampled for the species and from where records are likely to have been submitted to GBIF. We assigned a value of ten to the polygons and one to the remaining study area, indicating that areas contained within the polygons were ten times more likely to have been sampled.

Species Distribution Modelling Procedures

We generated two types of species distribution models (SDMs): climate models, which were projected to 2050 to study how climate and land cover changes (extrapolated based on the effects of climate change and human impacts) will affect the distribution of suitable conditions for the two species, and full present models, which included more fine-scale land cover variables with no future counterparts. Outputs of the full SDMs for *P. leo* were included in the *L. pictus* model to study the effect of including biotic interactions, in the form of the distribution of competitors, on model performance. We also compared the performance of our SDMs to a climate-only model, including only climatic and topographic variables, because this model type is commonly used in SDM studies of mammals to predict the effects of future environmental changes on species suitable ranges (e.g. Peterson et al., 2014; Razgour et al., 2013, 2015).

The modelling extent was set as Sub-Saharan Africa (Fig. 1). This area was chosen because it covered the majority of the currently known range of the two species (Woodroffe and Sillero-Zubiri, 2012). The resolution of the models was set as 5 arc minutes (approximately 10 km) to reflect the ranging behaviour of the species. The following environmental layers were downloaded from online databases: climatic and topography layers (WorldClim, www.worldclim.org/download); karst regions of the world (www.arcweb.forest.usf.edu/flex/KarstRegions); land cover (GlobCover2009, www.due.esrin.esa.int/globcover); Normalised Difference Vegetation index (NDVI, MODIS, www.glc.f.umd.edu/data/ndvi); human population density (www.ornl.gov/sci/landscan); water bodies (ESRI); and IMAGE3 land cover projections (Stehfest et al., 2014, www.pbl.nl/image). Land cover maps were reclassified to reduce the number of different categories. The IMAGE3 land cover layer had a coarser resolution than the models (~50 km), but it included projections of land cover changes for 2050 based on predicted future climate change and human impacts (Global Biodiversity Outlook, GBO4, Stehfest et al., 2014). Distance variables were generated for each land cover type from the finer resolution (~1 km) GlobCover layer to be used in the full present models. NDVI maps were split into the wet and dry season and averaged across years. A slope layer was generated from the

altitude map. Because collinearity can negatively affect variable estimation and model predictions (Merow et al., 2013), we removed highly correlated variables ($R > 0.8$, analysis carried out in ENMTools, Warren et al., 2010), as well as variables that did not contribute to the models. A total of 15 variables were used across the two SDM types and species (Tab. S1).

Model parameters were tested by altering the regularization value (1, 1.5, 2 and 3) and the number of modelling features included, and comparing model performance based on Akaike Information Criterion (AIC) scores in ENMTools (AICc for *L. pictus* due to low number of records). It is important to explore a range of regularization values, as default values maximise the measure of fit across a range of taxonomic groups and may not be appropriate for the target species (Merow et al., 2013). The best fit models across species included a regularization value of 1 and the first 3 features (linear, quadratic and product). The final model for each species was validated using five-fold cross-validations due to the low number of location records, to generate average AUC train and test values. AUC is a measure of predictive accuracy that indicates the model's ability to distinguish between presence and absences, or in the case of presence-only modelling, between presence and background (pseudo-absences; Merow et al., 2013). SDM AUC values were compared to randomly generated null models (generated in ENMTools with the altitude layer) to determine whether models performed significantly better than random, i.e. SDM AUC values fell outside the 95% confidence intervals of the distribution of the AUC values of 100 null models (Raes and ter Steege, 2007).

Climatic SDMs were projected into the future (2050) using variables that have corresponding future layers (climatic variables and the IMAGE3 land cover layer) and variables that are unlikely to change in the near future (topographic and geological variables). Future projections for 2050 were performed with four General Circulation Models: ACCESS1-0, BCC-CSM1-1, CCSM4, and HadCM3 (www.worldclim.org/download) using the IPCC5 ± 8.5 W/m² Representative Concentration Pathways (IPCC, 2013), representing the “worst case” scenario, whereby human consumption of fossil fuels is expected to remain the same as at present.

Niche and Range Overlap

Model outputs were processed in ENMTools to calculate the degree of niche overlap between the two species using Schoener's measure of niche similarity. Schoener's D measures the similarity among ecological models by comparing the estimates of habitat suitability calcu-

lated for each grid cell of the study area and normalising each model so that all suitability scores add up to 1 (Warren et al., 2010). We used the niche identity test in ENMTools to assess whether niche overlap is significantly different from random by comparing observed values to 20 randomised null datasets. Range overlap and extent of changes in suitable range and range overlap between current and future conditions were calculated in ArcGIS v10 (ESRI). Continuous SDM output maps were reclassified into binary maps (suitable/unsuitable) using the thresholding method that maximises the sum of sensitivity and specificity because it is particularly suitable for presence-only data and was found to have better discrimination ability than other thresholding methods (Liu et al., 2013).

Results

Species Distribution Modelling Outputs

All SDMs had high predictive ability (Full models: $AUC_{train}=0.88$, 0.87 , $AUC_{test}=0.81$, 0.77 ; Climate models: $AUC_{train}=0.84$, 0.79 , $AUC_{test}=0.80$, 0.72 ; for *L. pictus* and *P. leo*, respectively; Tab. 1) and performed significantly better than null models (Full null model AUC_{train} 95% Confidence Intervals=0.70–0.72; Climate null model AUC_{train} 95% CI=0.61–0.63). The inclusion of land cover variables

improved the predictive ability and performance of the *L. pictus* climate model (Climate-only model: $AUC_{train}=0.80$, $AUC_{test}=0.77$), and resulted in more refined projections, in particularly in southern Africa (Fig. 2).

Overall model projections of the probability of *L. pictus* occurrence were similar across SDMs. However, both climate models (climate-only and climate plus land cover) identified suitable areas for *L. pictus* south of the Congo Basin (in the Democratic Republic of Congo [DRC] and Congo), which were not identified as suitable by the full model, while only the full model identified suitable areas for *L. pictus* in Zambia and Malawi (Fig. 2). Projected range suitability based on the full model appears to better reflect the currently known range of the species (Fig. 1).

The full model identified that *L. pictus* has a higher probability of occurring in areas with low-medium temperatures during the coldest quarter (Bio11), low rainfall during the driest month (Bio14) and wet-test quarter (Bio16), in close proximity to conifer woodlands and barren areas, and relatively near urban areas. *L. pictus* was also found to be associated with the following land cover types: re-growing forest, grassland and scrubland (Tab. 1; Fig. S3).

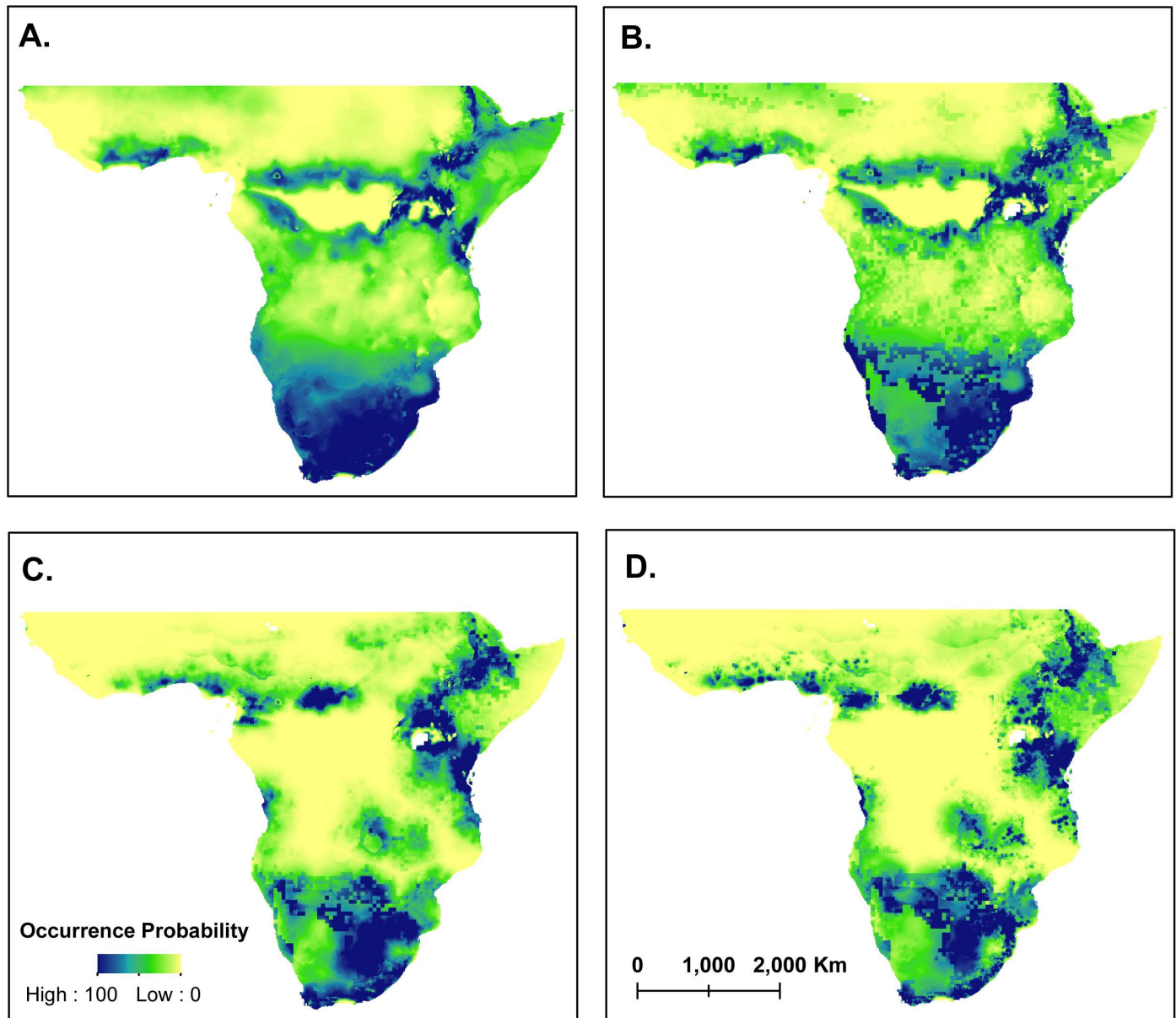


Figure 2 – Species distribution modelling predictions of relative occurrence probability of *Lycaon pictus* based on: A) the climate-only model, B) the climate model, including land cover variables with future projections (IMAGE 3 land cover), C) the full model, and D) when the predicted distribution of the dominant competitor, *Panthera leo*, is included in the full model. Relative occurrence probability ranges from high (100) in blue to low (0) in yellow.

Table 2 – The percent of the study area predicted to be suitable for *Lycaon pictus* and *Panthera leo* under present and future (2050) conditions, and percent change in range suitability.

Species	Present	2050	Change	% Reduction
<i>Lycaon pictus</i>	23.8%	13.4%	-10.4%	43.7%
<i>Panthera leo</i>	43.1%	28.6%	-14.5%	33.6%
Range overlap	58.4%	35.4%	-23.0%	39.4%

Land cover and distance to water bodies were the most important variables affecting habitat suitability for *P. leo*. Our models predicted that *P. leo* has a high probability of occurring in grasslands, scrublands, and tropical woodlands, near water bodies, but also near grasslands and barren areas. Other important variables were low annual precipitation (Bio12) and low mean temperature of the coldest quarter (Bio11; Tab. 1; Fig. S4).

Including Interspecific Competition

The *L. pictus* model including the distribution of its competitor had higher AUC scores ($AUC_{train}=0.90$), meaning that the inclusion of *P. leo* presence increases the predictive ability of the model. However, predictions of the occurrence probability of *L. pictus* remained relatively unchanged (Fig. 2). The same environmental variables were the main contributors to this model, but the relative occurrence probability of *P. leo* was one of the highest contributing variables (Tab. 1). The model predicted that *L. pictus* have a high probability of occurring in areas that are suitable for *P. leo*. Correspondingly, niche overlap between *L. pictus* and *P. leo* was significantly higher than expected by chance (observed Schoener's $D=0.63$; observed values fall outside the 95% confidence intervals of randomised null datasets: $D=0.49-0.56$). Moreover, 58.4% of the areas predicted to be suitable for *L. pictus* were also predicted to be suitable for *P. leo*.

Future Projections

Both species were predicted to experience substantial reductions in the extent of suitable areas by 2050 (Fig. 3), with *P. leo* maintaining a larger extent of suitable areas despite a 33.6% reduction in suitable range (Tab. 2). *L. pictus* is predicted to experience range contractions in Southern Africa (Namibia, Botswana and Zimbabwe) alongside range fragmentations in Central and East Africa, resulting in its range contracting by 43.7%. Range suitability for *P. leo* is predicted to decrease in particular in West and Central Africa, but remain largely unchanged in the south. Future projections for *L. pictus* and *P. leo* in small areas in West and East Africa are affected by variables outside their training range, in particular low mean temperature of the coldest quarter (Bio11), and so must be treated with caution (Fig. S5, S6). Niche overlap between *L. pictus* and *P. leo* is predicted to decrease by 2050 (Schoener's $D=0.56$). Range overlap is also predicted to decrease substantially, by 39.4% (to 35.4%), in particularly in Central and East Africa (Fig. 4; Tab. 2).

Discussion

Range suitability for the endangered African wild dog, *L. pictus*, is limited by climatic and land cover variables, as well as high niche and range overlap with its dominant competitor, *P. leo*, and therefore changing competitor range suitability due to climate change will affect the future distribution of *L. pictus*. SDMs have been used to monitor and predict the effects of environmental changes on the distributions of various species in Africa, from threatened acridivorous avian raptors overwintering in the Sahel (Augiron et al., 2015) to the malaria vector *Anopheles arabiensis* (Drake and Beier, 2014). However, to the best of our knowledge, this is the first study to take into account the effect of biotic interactions on the realised distributions of African species.

Environmental Variables Affecting Range Suitability

L. pictus has a high probability of occurring near barren areas, where temperatures during the cold quarter and precipitation during the driest

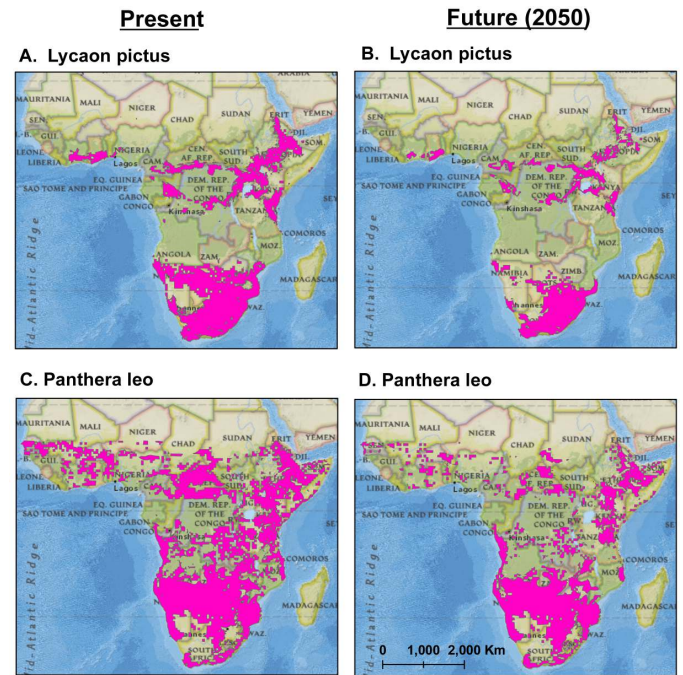


Figure 3 – Predicted changes in relative occurrence probability of the two studied species under present and future (2050) conditions: *Lycaon pictus* present (A) and future (B), and *Panthera leo* present (C) and future (D). A thresholding method was used to convert relative occurrence probabilities into suitable areas, which are marked in pink and presented over a National Geographic base map (ESRI).

month are relatively low, and is predominantly associated with regrowing forest, grassland and scrubland. Over a substantially smaller spatial extent, Whittington-Jones et al. (2014) also identified scrubland and woodland as the preferred land cover for *L. pictus*, and suggested that patterns of habitat selection are related to prey preferences. However, *L. pictus* has been shown to inhabit areas with low prey densities in an attempt to avoid interspecific competition (Van Der Meer et al., 2011). Avoidance of interspecific competition can explain our SDM predictions that *L. pictus* are found on the fringe of barren areas where prey densities are lower, but as a result the density of other competing carnivores is also reduced. This highlights the importance of distinguishing the realised niche, which is occupied by the species, from the potential niche predicted by SDMs.

Our models suggest that *P. leo* and *L. pictus* have similar land cover preferences, highlighting the potential for range overlap and interspecific competition for prey resources. Consistent with previous studies (Abade et al., 2014a; Schuette et al., 2013; Watson et al., 2015), we found that *P. leo* has a high probability of occurring in grasslands, scrublands and tropical woodlands, near water bodies, and where annual precipitation is low. Modelling the distribution of *P. leo* in Africa, Celesia et al. (2010) predicted that, similar to our findings, *P. leo* density would be highest in tropical savannah. However, contrary to our findings, they predicted that habitat suitability increases with increasing annual precipitation. Differences may arise because Celesia et al. (2010) only included location records from national parks and protected areas, and therefore their dataset does not represent the complete distribution of *P. leo*. Moreover, unlike our study, they did not use a bias layer to account for unequal sampling efforts and unrepresentative distribution of location records. Differences in the coverage of location records could also explain why Celesia et al. (2010) predicted that suitable areas for *P. leo* do not occur in West and Central Africa, while our models identified potential suitable areas in these regions.

It should be noted, however, that models based on environmental variables may overestimate the distribution of species because extirpation as a result of persecution by humans is not taken into account. For example, it has been shown that the presence of *P. leo* could not be reconfirmed in several Lion Conservation Units, primarily in West and Central Africa (Riggio et al., 2012; Henschel et al., 2014), and several

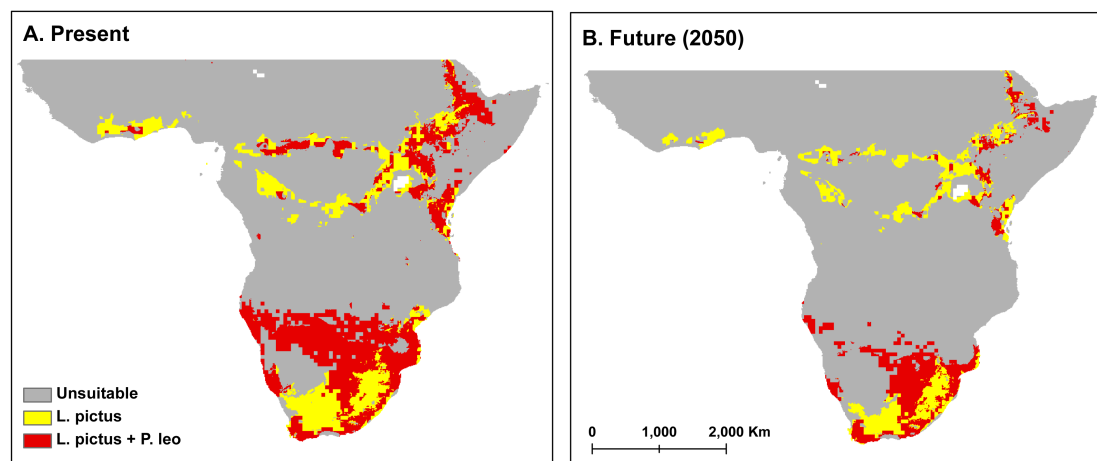


Figure 4 – Predicted change in range overlap between *Lycaon pictus* and *Panthera leo* under present (A) and future (2050; B) conditions.

other populations show a decline that can lead to future local extinctions (Bauer et al., 2015).

Future Climate and Land Cover Changes

Projected future climate and land cover changes are predicted to result in decreased range suitability for *L. pictus* by 2050, particularly in the south (Namibia, Botswana, Zimbabwe and Mozambique). Predicted range fragmentation in Namibia and Botswana is a major cause for conservation concern because of the typically large home ranges of this species (Kingdon and Hoffman, 2013). Fragmentation will force *L. pictus* to either inhabit unsuitable areas or break into smaller packs roaming over smaller home ranges. Small populations can experience loss of genetic diversity and inbreeding and are subject to higher risk of extinction from stochastic and demographic processes (Leigh et al., 2012). Therefore, without conservations management to increase connectivity, these areas may not be viable for *L. pictus* populations in the long-term. The extensive forest-savannah mosaic north of the Congo Basin is geographically isolated from other similar habitats, and while predicted to remain suitable for *L. pictus*, this species is thought to be locally extinct in this region and is unlikely to be able to cross the vast areas of intervening unsuitable habitats to recolonise this area (Henschel et al., 2014).

P. leo is also predicted to experience large reductions in its suitable range, particularly in West (Senegal, Mali and Burkina Faso) and Central Africa (Chad and Central African Republic) accompanied by range fragmentation across East Africa. Although this suggests the possibility of a release from the effect of competition in areas remaining suitable for *L. pictus* but predicted to become unsuitable for its competitor, interspecific competition is likely to intensify in areas predicted to remain suitable for the two species.

Peterson et al. (2014) predicted similar declines in *P. leo* range suitability in West Africa, but contrary to our findings they also predict declines in the south. As our study includes location records that better represent the true range of *P. leo* (Peterson et al. only used location records from national parks and reserves) and has corrected for sampling biases, our projections of future habitat suitability are likely more accurate, being that they are based on the full range of climatic conditions currently experienced by the species. Our predicted decline in *P. leo* range is consistent with Bauer et al. (2015)'s population models that predicted a 67% probability of *P. leo* decline in West and Central Africa outside protected, fenced areas, and a 37% probability of populations in East Africa declining by half in the next two decades. In addition, in line with our projections of limited changes in habitat suitability in the south, in South Africa, where *P. leo* is largely found in fenced enclosures, the populations are not predicted to decline (Bauer et al., 2015). Therefore, in areas where SDMs predict severe range contractions and fragmentation, fenced reserves may be essential for the conservation and long-term survival of *P. leo* populations.

SDM predictions of changes to range suitability and range contractions under future climate change are not unique to *L. pictus* and *P. leo*. In Morocco, reductions in future suitable areas are predicted for 50% of endemic reptile species (Martinez-Freiria et al., 2013), while in West Africa, a substantial species turnover is predicted by 2100, including 42.5% of amphibians, 35.2% of birds and 37.9% of mammals (Baker et al., 2015). The predicted global trend of suitable range contractions and range shifts highlights the importance of understanding the impacts of future climate change on biodiversity.

The Role of Interspecific Competition

An important factor to consider when predicting the future potential distribution of *L. pictus* is the high degree of range and niche overlap with *P. leo*. The occurrence probability of *P. leo* was among the variables with the greatest contribution to the *L. pictus* full model, indicating that the two carnivores typically occupy similar niches. In addition to sharing a large proportion of their predicted suitable range, *L. pictus* and *P. leo* were also found to be associated with similar land cover types. The degree of overlap is not surprising given that the species have a similar carnivorous diet. Optimal hunting conditions have even caused *L. pictus* to adopt a more nocturnal activity period, mirroring the behaviour of *P. leo* (Cozzi et al., 2012). *L. pictus* are often subject to kleptoparasitism due to their smaller size, which creates tension between the species and can lead to competitive exclusion of *L. pictus* (Van Der Meer et al., 2011). Top predators such as *P. leo* can suppress populations of smaller predators like *L. pictus* even beyond the effect of direct kills and competition, suggesting that *L. pictus* populations are likely to be constrained by high densities of *P. leo* (Swanson et al., 2014). Thus although we found high levels of similarity in the predicted niches of the two species, the realised niche of *L. pictus* may be substantially smaller than its potential/predicted niche and shaped by biotic interactions.

Review of Modelling Methods

We aimed to highlight areas that will remain suitable for *L. pictus* with changing climates and land cover, and thus can be the primary focus of future conservation efforts for this endangered species. Consequently, our models incorporate future predictions of both climate and land cover changes. While this limits model projections to 2050, Baker et al. (2015) recommend that climate change models should focus on earlier projections as their predictions are more reliable.

We found that the inclusion of more fine-scale land cover variables in the full model resulted in projections that better reflect the currently known range of the species. The climate models predicted high probability of *L. pictus* occurrence in areas south of the Congo Basin. These areas were not identified as suitable by our full model, which also included the effect of distance to barren and urban areas and grasslands. Although a land cover variables was also included in the climate model

(IMAGE 3 land cover projections), the resolution of this variable was much coarser (50 km), and as a result it was unable to distinguish fine-scale patterns of habitat use.

Climate-only models have been criticised as insufficient for quantifying the impact of climate change on the distribution of species because other abiotic and biotic factors are equally important in determining a species' range (Araujo and Luoto, 2007). Stanton et al. (2012) recommend that variables, such as land use, that affect species distributions in full models should be incorporated into future projections. In our study, both including land cover variables with corresponding 2050 projections and incorporating the effects of competing species greatly improved model performance (in terms of AUC values), generating more reliable and accurate projections. Therefore the inclusion of land cover and other non-climatic variables with corresponding future projections is particularly important when predicting the effects of future climate change for species whose distributions are not solely limited by climate.

It is important to maintain realistic expectations of SDMs derived from coarse habitat maps and re-scaled General Circulation Models. Although they highlight potential suitable habitats on the broad landscape scale, they can be much less accurate when identifying fine-scale distributions (Loe et al., 2012). The inclusion of coarse land cover variables in our future projections may have resulted in models that are less fine-tuned. However, it has provided a better representation of the environmental conditions limiting the species' distributions, and is justifiable given the large extent of our study area and the ranging behaviour of the species.

Conservation Management for *Lycaon pictus*

Few of the *L. pictus* conservation efforts to date have addressed the impacts of climate and habitat changes. Conservation efforts in Southern Africa have focused on the creation of meta-populations through reintroduction into isolated reserves and combating negative attitudes of land owners towards the species through education programmes in an attempt to decrease human-wildlife conflicts. The setting of conservancies on private reserves has helped address conflicts through reducing the amount of livestock taken by *L. pictus*. This has been successful in Save Valley in Zimbabwe, where the reintroduced population of *L. pictus* expanded to an estimated 190 individuals in less than 15 years (Lindsey et al., 2005a,b). Ecotourism has also been suggested as a conservation strategy for *L. pictus* in South Africa. However although tourists ranked *L. pictus* as a top attraction in Hluhluwe-iMfolozi Park, local opinion was largely negative towards the species and opposed its reintroduction (Gusset et al., 2008). In East Africa conservation strategies for the species have focused on protection against canine distemper and rabies infections by managing populations of domestic dog "reservoir" hosts (Woodroffe et al., 2012).

Thus, while studies have acknowledged the need to conserve biodiversity in face of global climate change (Hayward, 2009), there are no conservation management measures in place to address future changes in habitat suitability for *L. pictus*. The predicted range shifts, range contraction and subsequent habitat fragmentation based on our SDMs highlight the need for developing such adaptive conservation plans taking into account the distribution of both *L. pictus* and its competitors.

The decline in habitat suitability for *P. leo* in West, Central and East Africa could be beneficial for *L. pictus* populations, allowing them to exploit their full potential niche. Thus conservation efforts for *L. pictus* in the Sahel and tropical savannahs south of the Sahara and in East Africa should concentrate on maintaining habitat connectivity to provide space for larger packs to roam and enable populations to expand in face of release from interspecific competition. These regions can be the focus of conservation management to promote the establishment of long-term viable *L. pictus* populations. In Southern Africa, connected suitable areas are predicted to remain under future climate change, but they overlap with the predicted future *P. leo* distribution. Conservation measures in this area should focus on enabling *L. pictus* to coexist with its competitors through maintaining large pack sizes that can withstand kleptoparasitism (Darnell et al., 2014).

Phylogeographic data can further contribute to guiding conservation management aimed to maintain intraspecific diversity. Areas that remain climatically suitable under past episodes of climate change (glacial refugia) are likely to contain high levels of genetic diversity and distinct phylogenetic lineages because populations have persisted there across evolutionary times (Hewitt, 2000). Upper Guinea, the Cameroon Highlands, Congo Basin, Ethiopian Highlands, Anglo-Namibia area, and the south-eastern part of South Africa were identified as cross-taxonomic glacial refugia for 537 mammal and 1265 bird species (Levinsky et al., 2013). Loss of range suitability in glacial refugia under future climate change is a particular concern for long-term species conservation (Razgour et al., 2013). The fact the predicted *L. pictus* future range maintains some of the main refugia identified by Levinsky et al. (2013) is a cause for optimism in terms of the future viability and conservation of this endangered species. In contrast, *P. leo* is predicted to lose many of the refugia in the West and East by 2050. Phylogeographic studies show that *P. leo* populations in West and Central Africa represent a unique phylogenetic unit (Bertola et al., 2011, 2015), and therefore their loss will have wider implications for the long-term conservation of this species.

Conclusions

This study contributes to understanding the potential present and future range of the endangered *L. pictus* and the factors that limit its distribution, from climatic and land cover variables to interspecific interactions with its dominant competitor *P. leo*. Through determining changes in range suitability and range overlap, our SDMs helped identify priority areas for the sustainable conservation of *L. pictus*, and highlighted the importance of accounting for biotic interactions when predicting the future distribution of species.

We show that the fate of *L. pictus* is uncertain. *L. pictus* is threatened by persecution from humans, habitat loss and fragmentation, and the negative effects of interspecific competition with *P. leo*. Projected changes in climate are predicted to further reduce its suitable range by 2050, intensifying existing threats. However, East and Central African populations could be sustained due to the predicted loss of habitat suitability for *P. leo* in those regions. Hence, while overall range suitability for *L. pictus* is predicted to decline, future conservation management efforts can help promote the establishment of long-term, viable populations. 🐾

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Variables used in the species distribution models, with their respective codes and sources.

Figure S2 Variables included in the full and climatic *Lycaon pictus* SDMs and their relative contribution to the model.

Figure S3 Variables included in the full and climatic *Panthera leo* SDMs and their relative contribution to the model.

Figure S4 Areas where *Lycaon pictus* model predictions are affected by variables outside their training range when projected to 2050 (+8.5 rcp scenario).

Figure S5 Areas where *Panthera leo* model predictions are affected by variables outside their training range when projected to 2050 (+8.5 rcp scenario).