

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

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21 **Running title:** Predictive distribution modelling African wold dogs and competitors

22

23 **Abstract**

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

41

42 **Keywords:** Carnivores; Ecological interactions; Global biodiversity databases; Global change; *Lycaon*  
43 *pictus*; Niche overlap; *Panthera leo*; Species Distribution Modelling

## 44 **Introduction**

45 Climate change is recognised as the greatest impending threat to biodiversity across biomes (Millennium  
46 Ecosystem Assessment 2005), and therefore predicting its impacts on species is a top conservation  
47 priority (Thuiller et al. 2008). Global trends in hydrology indicate that some regions, like Southern Africa,  
48 are expected to suffer critical water stress under future climate change due to increased frequency of  
49 extreme conditions, such as floods and droughts (Dallas and Rivers-Moore 2014). Global temperatures  
50 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  
51 end of this century, leading to the expansion and contraction of climatic zones and shifts in species'  
52 ranges (Langer et al. 2013).

53 Apex predators play an important role in regulating ecological interactions, maintaining ecosystem health  
54 and influencing lower trophic levels (Bruno and Cardinale 2008; Schmitz et al. 2010). Their removal or  
55 disappearance can result in a loss of biodiversity and species richness across the ecosystem (Abade et al.  
56 2014b). African wild dogs, *Lycaon pictus*, have been present in Africa since the Plio-Pleistocene, with  
57 fossil records dating back 2-3 million years in sub-Saharan Africa. At present, the population of free-  
58 ranging *L. pictus* is estimated at less than 8000 individuals and the species is classified as Endangered by  
59 the IUCN (Woodroffe and Sillero-Zubiri 2012). Human population expansion, prey availability and  
60 interspecific competition are thought to be some of the main factors limiting the areas which the species  
61 can safely inhabit. *L. pictus* has large home ranges ( $150\text{-}2000\text{ km}^2$ , depending on habitat) and is thought to  
62 use a variety of habitats, including woodland, bushy savannah, semi-desert, and short-grass plains  
63 (Kingdon and Hoffman 2013).

64 Because *L. pictus* naturally occurs at low densities over vast ranges, habitat loss and fragmentation are  
65 major threats to its survival (Woodroffe and Ginsberg 1999). Large carnivore habitat has been reduced  
66 dramatically across the African savannah, with some areas experiencing losses of over 75% (Watson et al.  
67 2015). Many of the existing national parks and reserves may not be large enough to support viable  
68 populations of *L. pictus*. Reserves smaller than  $10000\text{ km}^2$  introduce edge effects (Woodroffe and  
69 Ginsberg 1999) and packs can move beyond the boundary of reserves into human populated areas (Van  
70 Der Meer et al. 2011), increasing the incidence of human-wildlife conflict. Hence it is important to  
71 understand the anthropogenic and ecological factors influencing habitat suitability and range preferences

72 of African carnivores in general (Kolowski and Holekamp 2009), and in particular species like *L. pictus*  
73 that are becoming increasingly endangered and in need of guided conservation efforts. Future climate  
74 change is likely to amplify threats to *L. pictus* due to habitat fragmentation, further enhancing the  
75 importance of understanding the factors limiting the species range and identifying important areas for  
76 future conservation efforts (Watson et al. 2015).

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

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

100 Specifically, SDMs can help guide species long-term conservation efforts through identifying future  
101 suitable areas and predicting loss of current habitats (Schwartz 2012).

102 Because species' ranges are rarely at equilibrium with climate, SDMs should incorporate other variables.  
103 Biotic interactions, such as interspecific competition, are important for identifying the realised niche of a  
104 species, i.e. the niche a species actually occupies as opposed to the niche it can theoretically occupy  
105 (Gillson et al. 2013). Incorporating interspecific competition from dominant species can improve the  
106 statistical modelling of species distributions (Austin 2002). The role of biotic interactions was once  
107 thought to only shape species distributions at local spatial scales, but it is now recognised that these  
108 interactions have left their mark on the distribution of species from local to global scales (Wisiz et al.  
109 2013). Recent studies have expressed the need for interspecific competition to be addressed when  
110 studying the range of carnivores (Van Der Meer et al. 2011; Vanak et al. 2013).

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

## 122 **Methods**

123 The potential distributions of the two study species, *L. pictus* and *P. leo*, were modelled under current and  
124 future conditions using the presence-only species distribution modelling approach Maxent (Phillips et al.,  
125 2006). Maxent was consistently found to out-perform other modelling methods, in terms of higher Area  
126 Under the Receiver Operator Curve (AUC) scores (Khatchikian, et al. 2010), better predictive ability  
127 (Elith et al. 2006) and not over-fitting suitable ranges (Peterson et al. 2007).

## 128 **Location Records**

129 Location records were downloaded from Global Biodiversity Information Facility (GBIF, [www.gbif.org](http://www.gbif.org))  
130 for the two species, and were supplemented with records from published papers (Celesia et al. 2010;  
131 Githiru et al. 2014; Malcolm and Siller-Zubiri 2001; Peterson et al. 2014) and from direct observations by  
132 researchers. We excluded records older than 1970 and any records with inaccurate coordinates to ensure  
133 the best representation of current distributions within the study area. Biodiversity databases like GBIF are  
134 often criticised for being spatially biased due to unequal sampling efforts or record submission among  
135 countries and geographical areas. Such bias can distort our view of large-scale biodiversity patterns (Beck  
136 et al. 2014). Because spatial autocorrelation and surplus records can result in imprecise models and poor  
137 quality outputs (Miller 2012) we used the nearest neighbour analysis in ArcGIS v10 (ESRI) to remove  
138 spatially clustered records. Maxent requires an unbiased dataset, and while many records were removed  
139 during nearest neighbour analysis, spatial sampling bias often cannot be avoided due to the location of  
140 research centres and studies (Brown 2014). To counteract spatial biases and poor range representation due  
141 to the low number of available location records (*L. pictus* N = 38, *P. leo* N = 61), we generated bias layers  
142 to reflect uneven sampling efforts across the species' potential ranges. In ArcGIS we traced crude  
143 polygons containing 100 km buffer around clusters of location records within the same country to  
144 represent areas that are likely to have been sampled for the species and from where records are likely to  
145 have been submitted to GBIF. We assigned a value of ten to the polygons and one to the remaining study  
146 area, indicating that areas contained within the polygons were ten times more likely to have been  
147 sampled.

## 148 **Species Distribution Modelling Procedures**

149 We generated two types of species distribution models (SDMs): climate models, which were projected to  
150 2050 to study how climate and land cover changes (extrapolated based on the effects of climate change  
151 and human impacts) will affect the distribution of suitable conditions for the two species, and full present  
152 models, which included more fine-scale land cover variables with no future counterparts. Outputs of the  
153 full SDMs for *P. leo* were included in the *L. pictus* model to study the effect of including biotic  
154 interactions, in the form of the distribution of competitors, on model performance. We also compared the  
155 performance of our SDMs to a climate-only model, including only climatic and topographic variables,  
156 because this model type is commonly used in SDM studies of mammals to predict the effects of future

157 environmental changes on species suitable ranges (e.g. Peterson et al. 2014; Razgour et al. 2013; Razgour  
158 et al. 2015).

159 The modelling extent was set as Sub-Saharan Africa (Figure 1). This area was chosen because it covered  
160 the majority of the currently known range of the two species (Woodroffe and Sillero-Zubiri 2012). The  
161 resolution of the models was set as 5 arc minutes (approximately 10 km) to reflect the ranging behaviour  
162 of the species. The following environmental layers were downloaded from online databases: climatic and  
163 topography layers (WorldClim, [www.worldclim.org/download](http://www.worldclim.org/download)); karst regions of the world  
164 ([www.arcweb.forest.usf.edu/flex/KarstRegions](http://www.arcweb.forest.usf.edu/flex/KarstRegions)); land cover (GlobCover2009,  
165 [www.due.esrin.esa.int/globcover](http://www.due.esrin.esa.int/globcover)); Normalised Difference Vegetation index (NDVI, MODIS,  
166 [www.glc.f.umd.edu/data/ndvi](http://www.glc.f.umd.edu/data/ndvi)); human population density ([www.ornl.gov/sci/landscan](http://www.ornl.gov/sci/landscan)); water bodies  
167 (ESRI); and IMAGE3 land cover projections (Stehfest et al. 2014, [www.pbl.nl/image](http://www.pbl.nl/image)). Land cover maps  
168 were reclassified to reduce the number of different categories. The IMAGE3 land cover layer had a  
169 coarser resolution than the models (~50 km), but it included projections of land cover changes for 2050  
170 based on predicted future climate change and human impacts (Global Biodiversity Outlook, GBO4,  
171 Stehfest et al. 2014). Distance variables were generated for each land cover type from the finer resolution  
172 (~1 km) GlobCover layer to be used in the full present models. NDVI maps were split into the wet and  
173 dry season and averaged across years. A slope layer was generated from the altitude map. Because  
174 collinearity can negatively affect variable estimation and model predictions (Merow et al. 2013), we  
175 removed highly correlated variables ( $R > 0.8$ , analysis carried out in ENMTools, Warren et al. 2010), as  
176 well as variables that did not contribute to the models. A total of 15 variables were used across the two  
177 SDM types and species (Supplementary Table S1).

178 Model parameters were tested by altering the regularization value (1, 1.5, 2 and 3) and the number of  
179 modelling features included, and comparing model performance based on Akaike Information Criterion  
180 (AIC) scores in ENMTools (AICc for *L. pictus* due to low number of records). It is important to explore a  
181 range of regularization values, as default values maximise the measure of fit across a range of taxonomic  
182 groups and may not be appropriate for the target species (Merow et al. 2013). The best fit models across  
183 species included a regularization value of 1 and the first 3 features (linear, quadratic and product). The  
184 final model for each species was validated using five-fold cross-validations due to the low number of  
185 location records, to generate average AUC train and test values. AUC is a measure of predictive accuracy

186 that indicates the model's ability to distinguish between presence and absences, or in the case of presence-  
187 only modelling, between presence and background (pseudo-absences; Merow et al. 2013). SDM AUC  
188 values were compared to randomly generated null models (generated in ENMTools with the altitude  
189 layer) to determine whether models performed significantly better than random, i.e. SDM AUC values  
190 fell outside the 95% confidence intervals of the distribution of the AUC values of 100 null models (Raes  
191 and ter Steege 2007).

192 Climatic SDMs were projected into the future (2050) using variables that have corresponding future  
193 layers (climatic variables and the IMAGE3 land cover layer) and variables that are unlikely to change in  
194 the near future (topographic and geological variables). Future projections for 2050 were performed with  
195 four General Circulation Models: ACCESS1-0, BCC-CSM1-1, CCSM4, and HadCM3  
196 ([www.worldclim.org/download](http://www.worldclim.org/download)) using the IPCC5 +8.5 W/m<sup>2</sup> Representative Concentration Pathways  
197 (IPCC, 2013), representing the 'worst case' scenario, whereby human consumption of fossil fuels is  
198 expected to remain the same as at present.

### 199 **Niche and Range Overlap**

200 Model outputs were processed in ENMTools to calculate the degree of niche overlap between the two  
201 species using Schoener's measure of niche similarity. Schoener's D measures the similarity among  
202 ecological models by comparing the estimates of habitat suitability calculated for each grid cell of the  
203 study area and normalising each model so that all suitability scores add up to 1 (Warren et al. 2010). We  
204 used the niche identity test in ENMTools to assess whether niche overlap is significantly different from  
205 random by comparing observed values to 20 randomised null datasets. Range overlap and extent of  
206 changes in suitable range and range overlap between current and future conditions were calculated in  
207 ArcGIS v10 (ESRI). Continuous SDM output maps were reclassified into binary maps  
208 (suitable/unsuitable) using the thresholding method that maximises the sum of sensitivity and specificity  
209 because it is particularly suitable for presence-only data and was found to have better discrimination  
210 ability than other thresholding methods (Liu et al. 2013).



## 227 **Results**

### 228 **Species Distribution Modelling Outputs**

229 All SDMs had high predictive ability (Full models:  $AUC_{train}=0.88, 0.87, AUC_{test}=0.81, 0.77$ ; Climate  
230 models:  $AUC_{train}=0.84, 0.79, AUC_{test} = 0.80, 0.72$ ; for *L. pictus* and *P. leo*, respectively; Table 1) and  
231 performed significantly better than null models (Full null model  $AUC_{train}$  95% Confidence Intervals =  
232 0.70-0.72; Climate null model  $AUC_{train}$  95% CI = 0.61-0.63). The inclusion of land cover variables  
233 improved the predictive ability and performance of the *L. pictus* climate model (Climate-only model:  
234  $AUC_{train}= 0.80, AUC_{test}= 0.77$ ), and resulted in more refined projections, in particularly in southern Africa  
235 (Figure 2).

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

242 The full model identified that *L. pictus* has a higher probability of occurring in areas with low-medium  
243 temperatures during the coldest quarter (Bio11), low rainfall during the driest month (Bio14) and wettest  
244 quarter (Bio16), in close proximity to conifer woodlands and barren areas, and relatively near urban areas.  
245 *L. pictus* was also found to be associated with the following land cover types: re-growing forest, grassland  
246 and scrubland (Table 1; Supplementary Figure S1).

247 Land cover and distance to water bodies were the most important variables affecting habitat suitability for  
248 *P. leo*. Our models predicted that *P. leo* has a high probability of occurring in grasslands, scrublands, and  
249 tropical woodlands, near water bodies, but also near grasslands and barren areas. Other important  
250 variables were low annual precipitation (Bio12) and low mean temperature of the coldest quarter (Bio11;  
251 Table 1; Supplementary Figure S2).

## 252 **Including Interspecific Competition**

253 The *L. pictus* model including the distribution of its competitor had higher AUC scores ( $AUC_{\text{train}}=0.90$ ),  
254 meaning that the inclusion of *P. leo* presence increases the predictive ability of the model. However,  
255 predictions of the occurrence probability of *L. pictus* remained relatively unchanged (Figure 2). The same  
256 environmental variables were the main contributors to this model, but the relative occurrence probability  
257 of *P. leo* was one of the highest contributing variables (Table 1). The model predicted that *L. pictus* have  
258 a high probability of occurring in areas that are suitable for *P. leo*. Correspondingly, niche overlap  
259 between *L. pictus* and *P. leo* was significantly higher than expected by chance (observed Schoener's  
260  $D=0.63$ ; observed values fall outside the 95% confidence intervals of randomised null datasets:  $D=0.49$ -  
261  $0.56$ ). Moreover, 58.4% of the areas predicted to be suitable for *L. pictus* were also predicted to be  
262 suitable for *P. leo*.

## 263 **Future Projections**

264 Both species were predicted to experience substantial reductions in the extent of suitable areas by 2050  
265 (Figure 3), with *P. leo* maintaining a larger extent of suitable areas despite a 33.6% reduction in suitable  
266 range (Table 2). *L. pictus* is predicted to experience range contractions in Southern Africa (Namibia,  
267 Botswana and Zimbabwe) alongside range fragmentations in Central and East Africa, resulting in its  
268 range contracting by 43.7%. Range suitability for *P. leo* is predicted to decrease in particular in West and  
269 Central Africa, but remain largely unchanged in the south. Future projections for *L. pictus* and *P. leo* in  
270 small areas in West and East Africa are affected by variables outside their training range, in particular low  
271 mean temperature of the coldest quarter (Bio11), and so must be treated with caution (Supplementary  
272 Figures S3-S4). Niche overlap between *L. pictus* and *P. leo* is predicted to decrease by 2050 (Schoener's  
273  $D=0.56$ ). Range overlap is also predicted to decrease substantially, by 39.4% (to 35.4%), in particularly in  
274 Central and East Africa (Figure 4; Table 2).

## 275 **Discussion**

276 Range suitability for the endangered African wild dog, *L. pictus*, is limited by climatic and land cover  
277 variables, as well as high niche and range overlap with its dominant competitor, *P. leo*, and therefore  
278 changing competitor range suitability due to climate change will affect the future distribution of *L. pictus*.

279 SDMs have been used to monitor and predict the effects of environmental changes on the distributions of  
280 various species in Africa, from threatened acridivorous avian raptors overwintering in the Sahel (Augiron  
281 et al. 2015) to the malaria vector *Anopheles arabiensis* (Drake and Beier 2014). However, to the best of  
282 our knowledge, this is the first study to take into account the effect of biotic interactions on the realised  
283 distributions of African species.

#### 284 **Environmental Variables Affecting Range Suitability**

285 *L. pictus* has a high probability of occurring near barren areas, where temperatures during the cold quarter  
286 and precipitation during the driest month are relatively low, and is predominantly associated with re-  
287 growing forest, grassland and scrubland. Over a substantially smaller spatial extent, Whittington-Jones et  
288 al. (2014) also identified scrubland and woodland as the preferred land cover for *L. pictus*, and suggested  
289 that patterns of habitat selection are related to prey preferences. However, *L. pictus* has been shown to  
290 inhabit areas with low prey densities in an attempt to avoid interspecific competition (Van Der Meer et al.  
291 2011). Avoidance of interspecific competition can explain our SDM predictions that *L. pictus* are found  
292 on the fringe of barren areas where prey densities are lower, but as a result the density of other competing  
293 carnivores is also reduced. This highlights the importance of distinguishing the realised niche, which is  
294 occupied by the species, from the potential niche predicted by SDMs.

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

308 It should be noted, however, that models based on environmental variables may overestimate the  
309 distribution of species because extirpation as a result of persecution by humans is not taken into account.  
310 For example, it has been shown that the presence of *P. leo* could not be re-confirmed in several Lion  
311 Conservation Units, primarily in West and Central Africa (Riggio et al. 2012; Henschel et al. 2014), and  
312 several other populations show a decline that can lead to future local extinctions (Bauer et al. 2015).

### 313 **Future Climate and Land Cover Changes**

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

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

332 Peterson et al. (2014) predicted similar declines in *P. leo* range suitability in West Africa, but contrary to  
333 our findings they also predict declines in the south. As our study includes location records that better  
334 represent the true range of *P. leo* (Peterson et al. only used location records from national parks and  
335 reserves) and has corrected for sampling biases, our projections of future habitat suitability are likely

336 more accurate, being that they are based on the full range of climatic conditions currently experienced by  
337 the species. Our predicted decline in *P. leo* range is consistent with Bauer et al.'s (2015) population  
338 models that predicted a 67% probability of *P. leo* decline in West and Central Africa outside protected,  
339 fenced areas, and a 37% probability of populations in East Africa declining by half in the next two  
340 decades. In addition, in line with our projections of limited changes in habitat suitability in the south, in  
341 South Africa, where *P. leo* is largely found in fenced enclosures, the populations are not predicted to  
342 decline (Bauer et al. 2015). Therefore, in areas where SDMs predict severe range contractions and  
343 fragmentation, fenced reserves may be essential for the conservation and long-term survival of *P. leo*  
344 populations.

345 SDM predictions of changes to range suitability and range contractions under future climate change are  
346 not unique to *L. pictus* and *P. leo*. In Morocco, reductions in future suitable areas are predicted for 50% of  
347 endemic reptile species (Martinez-Freiria et al. 2013), while in West Africa, a substantial species turnover  
348 is predicted by 2100, including 42.5% of amphibians, 35.2% of birds and 37.9% of mammals (Baker et al.  
349 2015). The predicted global trend of suitable range contractions and range shifts highlights the importance  
350 of understanding the impacts of future climate change on biodiversity.

### 351 **The Role of Interspecific Competition**

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

364 predicted niches of the two species, the realised niche of *L. pictus* may be substantially smaller than its  
365 potential/predicted niche and shaped by biotic interactions.

## 366 **Review of Modelling Methods**

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

372 We found that the inclusion of more fine-scale land cover variables in the full model resulted in  
373 projections that better reflect the currently known range of the species. The climate models predicted high  
374 probability of *L. pictus* occurrence in areas south of the Congo Basin. These areas were not identified as  
375 suitable by our full model, which also included the effect of distance to barren and urban areas and  
376 grasslands. Although a land cover variable was also included in the climate model (IMAGE 3 land cover  
377 projections), the resolution of this variable was much coarser (50 km), and as a result it was unable to  
378 distinguish fine-scale patterns of habitat use.

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

388 It is important to maintain realistic expectations of SDMs derived from coarse habitat maps and re-scaled  
389 General Circulation Models. Although they highlight potential suitable habitats on the broad landscape  
390 scale, they can be much less accurate when identifying fine-scale distributions (Loe et al. 2012). The  
391 inclusion of coarse land cover variables in our future projections may have resulted in models that are less

392 fine-tuned. However, it has provided a better representation of the environmental conditions limiting the  
393 species' distributions, and is justifiable given the large extent of our study area and the ranging behaviour  
394 of the species.

### 395 **Conservation Management for *Lycaon pictus***

396 Few of the *L. pictus* conservation efforts to date have addressed the impacts of climate and habitat  
397 changes. Conservation efforts in Southern Africa have focused on the creation of meta-populations  
398 through reintroduction into isolated reserves and combating negative attitudes of land owners towards the  
399 species through education programmes in an attempt to decrease human-wildlife conflicts. The setting of  
400 conservancies on private reserves has helped address conflicts through reducing the amount of livestock  
401 taken by *L. pictus*. This has been successful in Save Valley in Zimbabwe, where the reintroduced  
402 population of *L. pictus* expanded to an estimated 190 individuals in less than 15 years (Lindsey et al.  
403 2005a; 2005b). Ecotourism has also been suggested as a conservation strategy for *L. pictus* in South  
404 Africa. However although tourists ranked *L. pictus* as a top attraction in Hluhluwe-iMfolozi Park, local  
405 opinion was largely negative towards the species and opposed its reintroduction (Gusset et al. 2008). In  
406 East Africa conservation strategies for the species have focused on protection against canine distemper  
407 and rabies infections by managing populations of domestic dog 'reservoir' hosts (Woodroffe et al. 2012).

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

413 The decline in habitat suitability for *P. leo* in West, Central and East Africa could be beneficial for *L.*  
414 *pictus* populations, allowing them to exploit their full potential niche. Thus conservation efforts for *L.*  
415 *pictus* in the Sahel and tropical savannahs south of the Sahara and in East Africa should concentrate on  
416 maintaining habitat connectivity to provide space for larger packs to roam and enable populations to  
417 expand in face of release from interspecific competition. These regions can be the focus of conservation  
418 management to promote the establishment of long-term viable *L. pictus* populations. In Southern Africa,  
419 connected suitable areas are predicted to remain under future climate change, but they overlap with the

420 predicted future *P. leo* distribution. Conservation measures in this area should focus on enabling *L. pictus*  
421 to coexist with its competitors through maintaining large pack sizes that can withstand kleptoparasitism  
422 (Darnell et al. 2014).

423 Phylogeographic data can further contribute to guiding conservation management aimed to maintain  
424 intraspecific diversity. Areas that remain climatically suitable under past episodes of climate change  
425 (glacial refugia) are likely to contain high levels of genetic diversity and distinct phylogenetic lineages  
426 because populations have persisted there across evolutionary times (Hewitt, 2000). Upper Guinea, the  
427 Cameroon Highlands, Congo Basin, Ethiopian Highlands, Anglo-Namibia area, and the south-eastern part  
428 of South Africa were identified as cross-taxonomic glacial refugia for 537 mammal and 1265 bird species  
429 (Levinsky et al. 2013). Loss of range suitability in glacial refugia under future climate change is a  
430 particular concern for long-term species conservation (Razgour et al. 2013). The fact the predicted *L.*  
431 *pictus* future range maintains some of the main refugia identified by Levinsky et al. (2013) is a cause for  
432 optimism in terms of the future viability and conservation of this endangered species. In contrast, *P. leo* is  
433 predicted to lose many of the refugia in the West and East by 2050. Phylogeographic studies show that *P.*  
434 *leo* populations in West and Central Africa represent a unique phylogenetic unit (Bertola et al. 2011;  
435 2015), and therefore their loss will have wider implications for the long-term conservation of this species.

## 436 **Conclusions**

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

443 We show that the fate of *L. pictus* is uncertain. *L. pictus* is threatened by persecution from humans,  
444 habitat loss and fragmentation, and the negative effects of interspecific competition with *P. leo*. Projected  
445 changes in climate are predicted to further reduce its suitable range by 2050, intensifying existing threats.  
446 However, East and Central African populations could be sustained due to the predicted loss of habitat  
447 suitability for *P. leo* in those regions. Hence, while overall range suitability for *L. pictus* is predicted to



448 decline, future conservation management efforts can help promote the establishment of long-term, viable  
449 populations.

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620 Research Council (NERC) Independent Research Fellowship (NE/M018660/1).

621 **Table 1** – Environmental layers included in each of the species distribution models (Full = full model;  
622 Climate = climatic variables and IMAGE3 land cover variables; Full+Competitor = Full model plus  
623 competitor) for both species with the corresponding percent contribution, along with the average AUC  
624 test and train values. The climate models only incorporate the layers from the full models which have  
625 corresponding future projections. The *L. pictus* model with competitor includes all the layers from the *L.*  
626 *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 +<br>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                 | -       | -                   | -       |
| <b>AUC test</b>                             | 0.809                | 0.817                | 0.795   | 0.770               | 0.723   |
| <b>AUC train</b>                            | 0.884                | 0.900                | 0.842   | 0.865               | 0.786   |

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628



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

| <b>Species</b>       | <b>Present</b> | <b>2050</b> | <b>Change</b> | <b>% Reduction</b> |
|----------------------|----------------|-------------|---------------|--------------------|
| <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%              |

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632

633 **Figures**

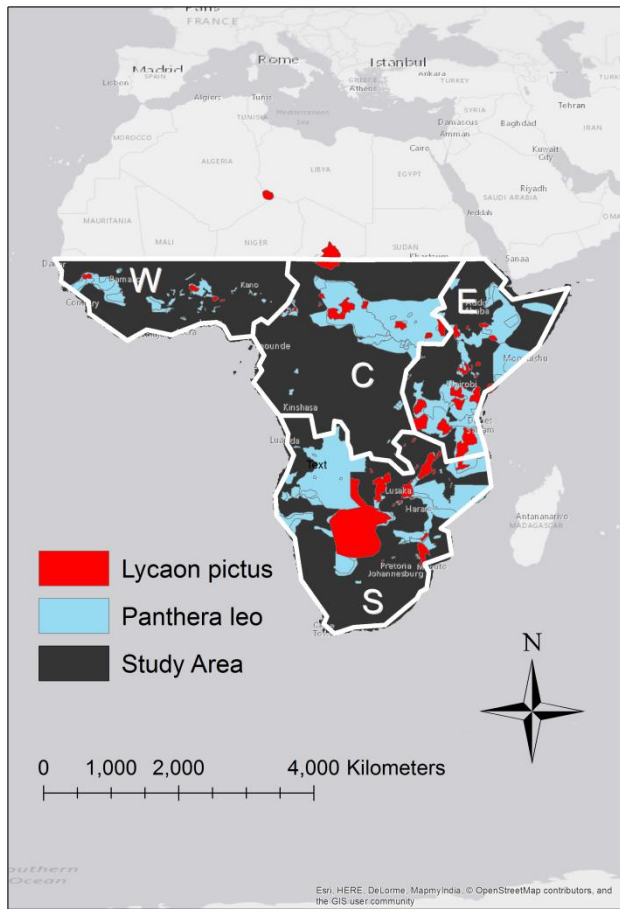
634 **Figure 1** – The selected study area (in black) and species known ranges based on the IUCN RedList  
635 (Woodroffe and Sillero-Zubiri, 2012), displayed over an OpenStreetMap base map (ESRI). The  
636 geographical regions referred to in the manuscript are marked in white (W=West, C=Central, E=East,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

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

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

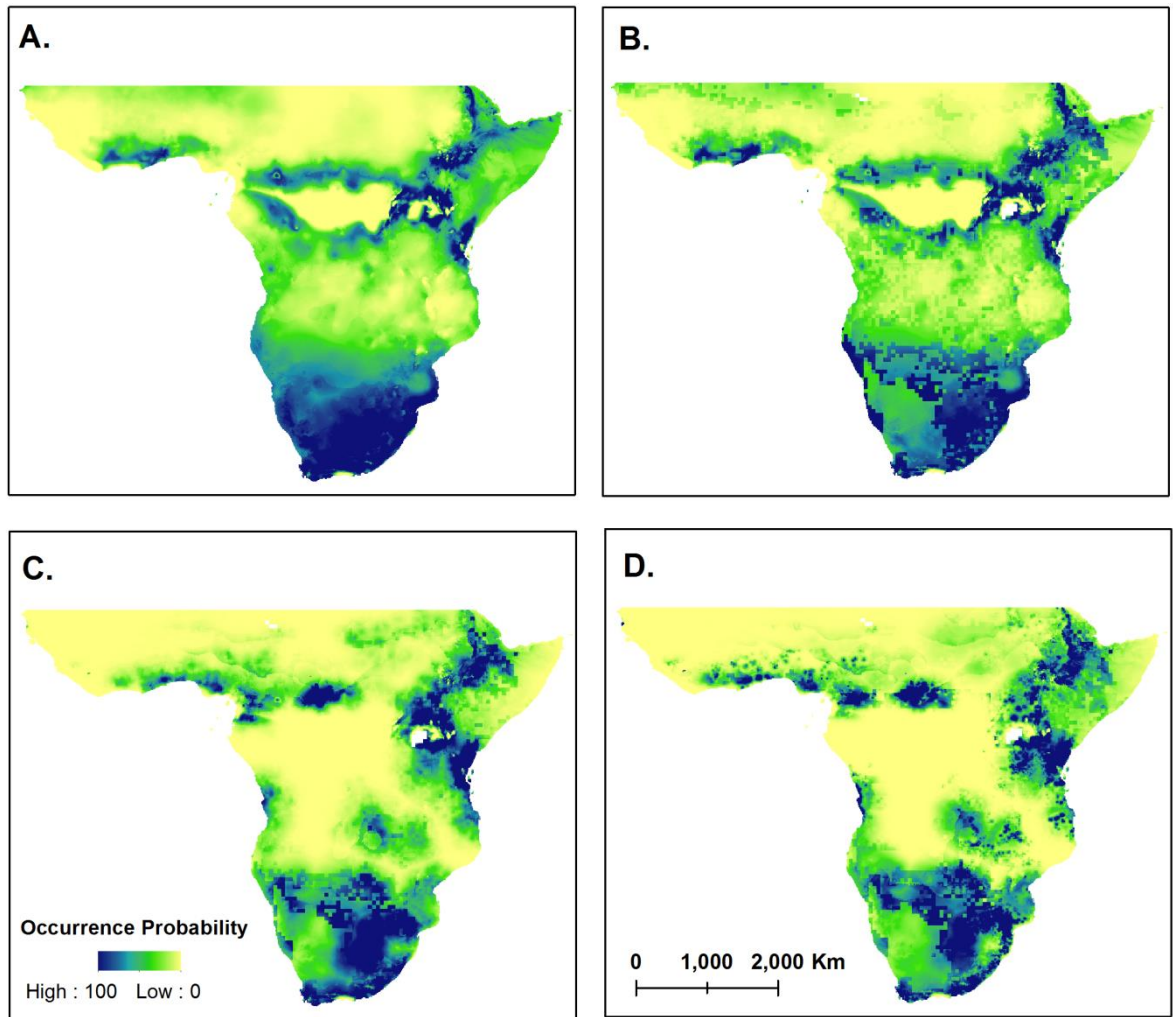
647 **Figure 4** – Predicted change in range overlap between *Lycaon pictus* and *Panthera leo* under present (A)  
648 and future (2050; B) conditions.

649 **Figure 1**



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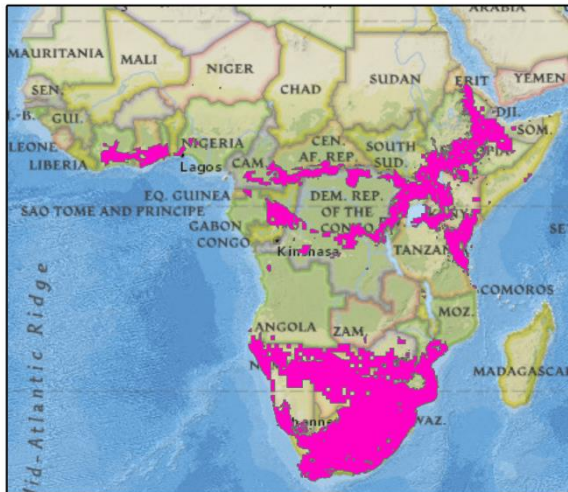


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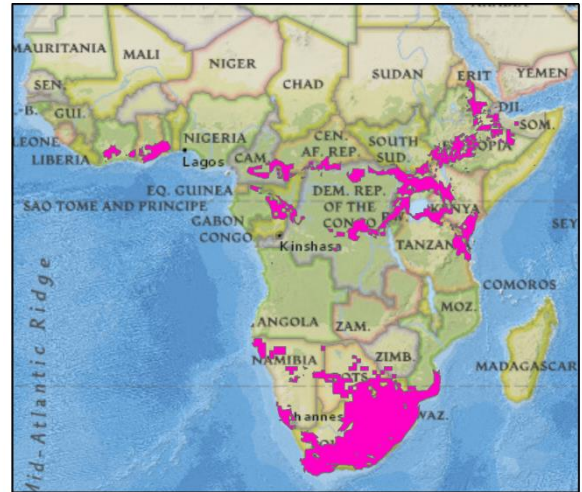
**Present**

**A. *Lycaon pictus***

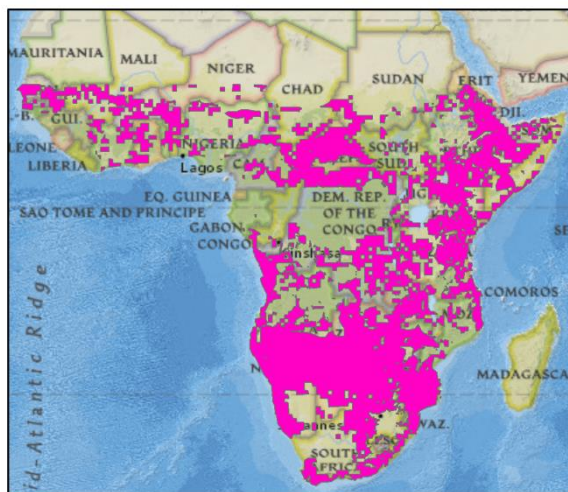


**Future (2050)**

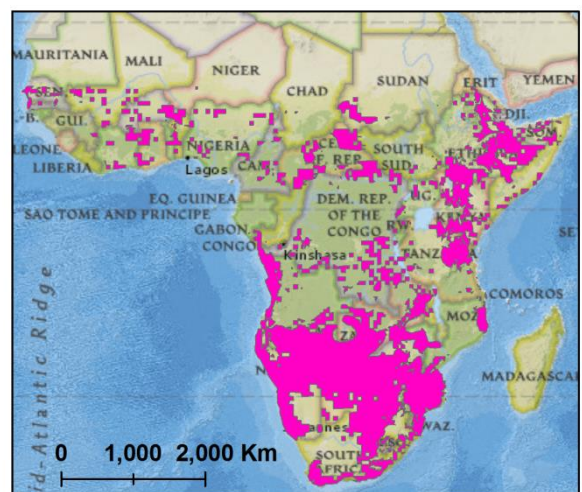
**B. *Lycaon pictus***



**C. *Panthera leo***



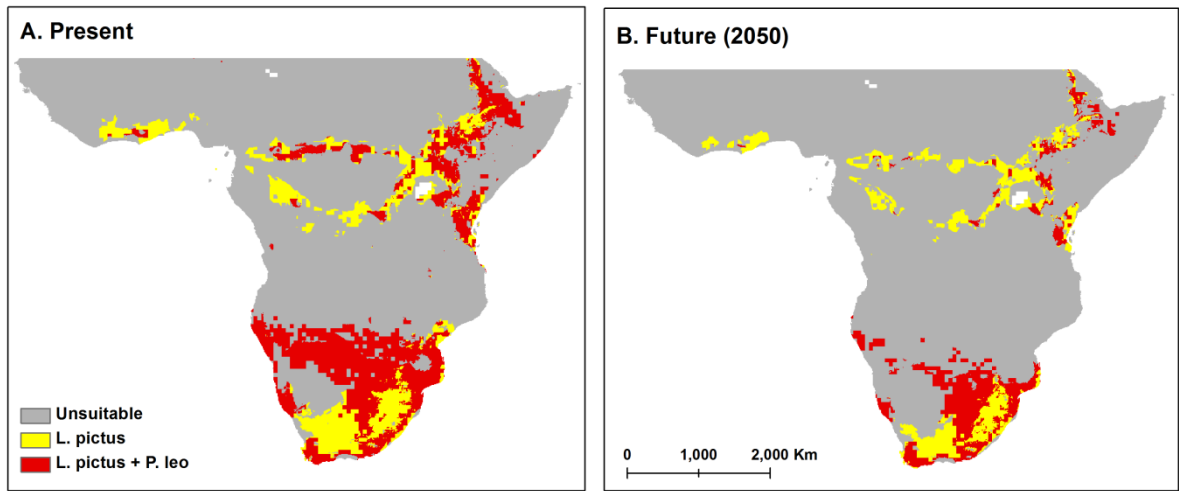
**D. *Panthera leo***



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658 **Figure 4**



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