

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

3 Megan Jones¹, Laura D. Bertola^{2,3}, Orly Razgour^{1,4}

4 ¹ Biological & Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK.

5 ² Institute of Environmental Sciences (CML), Leiden University, PO Box 9518, 2300 RA Leiden, The
6 Netherlands.

7 ³ Institute of Biology Leiden (IBL), Leiden University, PO Box 9505, 2300 RA Leiden, The Netherlands.

8 ⁴ School of Biological Sciences, University of Bristol, Life Sciences Building, Bristol BS8 1TQ, UK.

9

10 Corresponding author:

11 Orly Razgour

12 School of Biological Sciences

13 University of Bristol

14 Life Sciences Building

15 24 Tyndall Avenue

16 Bristol BS8 1TQ

17 UK

18 Tel: (+44) 0117-3941383

19 Email: Orly.Razgour@gmail.com

20

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 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)
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); karst regions of the world
164 (www.arcweb.forest.usf.edu/flex/KarstRegions); land cover (GlobCover2009,
165 www.due.esrin.esa.int/globcover); Normalised Difference Vegetation index (NDVI, MODIS,
166 www.glc.f.umd.edu/data/ndvi); human population density (www.ornl.gov/sci/landscan); water bodies
167 (ESRI); and IMAGE3 land cover projections (Stehfest et al. 2014, 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) using the IPCC5 +8.5 W/m² 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 ($AUC_{train}=0.90$),
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 variables 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.

450 **References**

- 451 Abade L., MacDonald D.W., Dickman A.J. 2014a. Assessing the relative importance of landscape and
452 husbandry factors in determining large carnivore depredation risk in Tanzania's Ruaha
453 landscape. *Biological Conservation* 180: 241-248
- 454 Abade L., MacDonald D.W., Dickman A.J. 2014b. Using Landscape and Bioclimatic Features to Predict
455 the Distributions of Lions, Leopards, and Spotted Hyaenas in Tanzania's Ruaha Landscape.
456 *PLoS ONE* 9: e96261
- 457 Araujo M.B., Luoto M. 2007. The importance of biotic interactions for modelling species distributions
458 under climate change. *Global Ecology and Biogeography* 16: 743-753
- 459 Augiron S., Gangloff B., Brodier S., Chevreux F., Blanc J. F., Pilard P., Coly A., Sonko A., Schlaich A.,
460 Bretagnolle V., Villers A. 2015. Winter spatial distribution of threatened acridivorous avian
461 predators: Implications for their conservation in a changing landscape. *Journal of Arid*
462 *Environments* 113: 145-153
- 463 Austin M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and
464 statistical modelling. *Ecological Modelling* 157: 101-118
- 465 Baker D.J., Hartley A.J., Burgess N.D., Butchart S.H.M., Carr J.A., Smith R.J., Belle E., Willis S.G.
466 2015. Assessing climate change impacts for vertebrate fauna across the West African protected
467 area network using regionally appropriate climate projections. *Diversity and Distributions* 21:
468 991-1003
- 469 Bauer H., Chapron G., Nowell K., Henschel P., Funston P., Hunter L.T.B., Macdonald D.W., Packer C.
470 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively
471 managed areas. *Proceedings of the National Academy of Sciences* 112: 14894-14899
- 472 Beck J., Boller M., Erhardt A., Schwanghart W., 2014. Spatial bias in the GBIF database and its effect on
473 modelling species' geographic distributions. *Ecological Informatics* 19: 10-15
- 474 Bertola L.D., van Hooft W.F., Vrieling K., Uit de Weerd D.R., York D.S., Bauer H., et al. 2011. Genetic
475 diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in
476 West and Central Africa. *Journal of Biogeography* 38: 1356–1367.

477 Bertola L.D., Tensen L., van Hooft P., White P.A., Driscoll C.A., Henschel P., et al. 2015. Autosomal and
478 mtDNA Markers Affirm the Distinctiveness of Lions in West and Central Africa. PLoS ONE 10:
479 e0137975.

480 Brambilla M., Casale F., Bergero V., Crovetto G.M., Falco R., Negri I., Siccardi P., Bogliani G. 2009.
481 GIS-models work well, but are not enough: Habitat preferences of *Lanius collurio* at multiple
482 levels and conservation implications. Biological Conservation 142: 2033-2042

483 Brown J.L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and
484 species distribution model analyses. Methods in Ecology and Evolution 5: 694-700

485 Bruno J.F., Cardinale B.J. 2008. Cascading effects of predator richness. Frontiers in Ecology and the
486 Environment 6: 539–546.

487 Celesia G.G., Peterson A.T., Kerbis-Peterhans J.C., Gnoske T.P. 2010. Climate and landscape correlates
488 of African lion (*Panthera leo*) demography, African Journal of Ecology 48: 58-71

489 Cozzi G., Broekhuis F., McNutt J. W., Turnbull L. A., Macdonald D.W., Schmid B. 2012. Fear of the
490 dark or dinner by moonlight? Reduced temporal partitioning among Africa’s large carnivores.
491 Ecology 93: 2590-2599

492 Dallas H.F., Rivers-Moore N. 2014. Ecological consequences of global climate change for freshwater
493 ecosystems in South Africa. South African Journal of Science 110

494 Darnell A.M., Graf J.A., Somer M.J., Slotow R., Gunther M.S. 2014. Space use of African wild dogs in
495 relations to other large carnivores. PLoS ONE 9: e98846

496 Drake J.M., Beier J.C. 2014. Ecological niche and potential distribution of *Anopheles arabiensis* in Africa
497 in 2050. Malaria Journal 13: 213

498 Elith J., Graham H., Anderson R.P., Dudik M., Ferrier S., Guisan A., et al. 2006. Novel methods improve
499 prediction of species’ distributions from occurrence data, Ecography 29: 129-151

500 Gillson L., Dawson T.P., Jack S., McGeoch M.A. 2013. Accommodating climate change contingencies in
501 conservation strategy. Trends in Ecology and Evolution 28: 135-142

502 Githiru M., Kasaine S., Mdamu D.M., Amakobe B. 2014. Recent records and conservation issues
503 affecting the African wild dogs in the Kasigau Corridor, south-east Kenya. Canid Biology and
504 Conservation 17: 1478-2677

505 Gusset M., Ryan S.J., Hofmeyr M., van Dyk G., Davies-Mostert H.T., Graf J.A., et al. 2008. Efforts
506 going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa.
507 Journal of Applied Ecology 45: 100-108

508 Hayward M.W. 2009. Conservation management for the past, present and future. Biodiversity and
509 Conservation 18: 765-775

510 Henschel P., Malanda G. A., Hunter L. 2014. The status of savannah carnivores in the Odzala-Kokoua
511 National Park, northern Republic of Congo. Journal of Mammalogy 95: 882-892

512 Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. Nature, 405: 907-913

513 IPCC 2013. Climate Change 2013: The Physical Science Basis. In: Stocker T.F., Qin D., Plattner G.K., et
514 al. (Eds.), Working Group I Contribution to the Fifth Assessment Report of the
515 Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and
516 New York, USA.

517 Jackson C.R., Power R.J., Groom R.J., Masenga E.H., Mjinga E.E., Fyumagwa R.D., Røskoft E., Davies-
518 Mostert H. 2014. Heading for the hills: Risk avoidance drives den site selection in African wild
519 dogs. PLoS ONE 9 (6): e99686.

520 Khatchikian C., Sangermano F., Kendell D., Livdahl T. 2010. Evaluation of species distribution model
521 algorithms for fine-scale container-breeding mosquito risk prediction, Medical and Veterinary
522 Entomology 25: 268-275

523 Kingdon J., Hoffman M. 2013. Genus *Lycaon*: African Wild Dog. Mammals of Africa. London:
524 Bloomsbury Publishing, 50-59

525 Kolowski J.M., Holekamp K.E. 2009. Ecological and anthropogenic influences on space use by spotted
526 hyaenas. Journal of Zoology 277: 23-36

527 Langer M.R., Weinmann A.E., Lotters S., Bernhard J.M., Rodder D. 2013. Climate-driven range extension
528 of *Amphistegina* (Protista, Foraminiferida): Models of current and predicted future ranges. PLoS
529 ONE 8(2): e54443.

530 Leigh K.A., Zenger K.R., Tammen I., Raadsma H.W. 2012. Loss of genetic diversity in an outbreeding
531 species: Small population effects in the African wild dog (*Lycaonpictus*). Conservation Genetics
532 13: 767-777

533 Levinsky I., Araujo M.B., Nogues-Bravo D., Haywood A.M., Valdes P.J., Rahbek C. 2013. Climate
534 envelope models suggest spatio-temporal co-occurrence of refugia of African birds and
535 mammals, *Global Ecology and Biogeography* 22: 351-363

536 Lindsey P.A., du Toit J.T., Mills M.G.L. 2005a. Attitudes of ranchers towards African wild dogs *Lycaon*
537 *pictus*: Conservation implications on private land. *Biological Conservation* 125: 113-121

538 Lindsey P.A., Alexander R.R., du Toit J.T., Mills M.G.L. 2005b. The potential contribution of ecotourism
539 to African wild dog *Lycaon pictus* conservation in South Africa. *Biological Conservation* 123:
540 339-348

541 Liu C., White M., Newell G. 2013. Selecting thresholds for the prediction of species occurrence with
542 presence-only data. *Journal of Biogeography* 40: 778-789

543 Loe L.E., Bonenfant C., Meisingset E.L., Myserud A. 2012. Effects of spatial scale and sample size in
544 GPS-based species distribution models: are the best models trivial for red deer management?
545 *European Journal of Wildlife Research* 58: 195-203

546 Malcolm J.R., Sillero-Zubiri C. 2001. Recent records of African wild dogs (*Lycaon pictus*) from Ethiopia.
547 *Canid News* 4. www.canids.org/canidnews/4/ethiopian_wild_dog.htm [Accessed on 23rd
548 November 2015].

549 Martinez-Freiria F., Argaz H., Fahd S., Brito J. 2013. Climate change is predicted to negatively influence
550 Moroccan endemic reptile richness. Implications for conservation in protected areas.
551 *Naturwissenschaften* 100: 877-889

552 Merow C., Smith M.J., Silander Jr. J.A. 2013. A practical guide to MaxEnt for modelling species'
553 distributions: what it does and why inputs and settings matter. *Ecography* 36: 1058-1069

554 Millennium Ecosystem Assessment 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*.
555 www.millenniumassessment.org/en/index.html [Accessed on 23rd November 2015].

556 Miller J.A. 2012. Species distribution models: Spatial autocorrelation and non-stationary. *Progress in*
557 *Physical Geography* 36: 681-692

558 Peterson A.T., Papes M., Eaton M. 2007. Transferability and model evaluation in ecological niche
559 modelling: a comparison of GARP and Maxent, *Ecography* 30: 550-560

560 Peterson A.T., Radocly T., Hall E., Kerbis-Peterhans J.C., Celesia G.G. 2014. The potential distribution of
561 the Vulnerable African lion *Panthera leo* in the face of changing global climate. *ORYX* 48: 555-
562 564

563 Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modelling of species geographic
564 distributions. *Ecological Modelling* 190: 231-259

565 Raes N., ter Steege H. 2007. A null-model for significance testing of presence-only species distribution
566 models. *Ecography* 30: 727-736

567 Razgour O., Juste J., Ibáñez C., Kiefer A., Rebelo H., Puechmaille S.J., Arlettaz R., Burke T., Dawson
568 D.A., Beaumont M., Jones G. 2013. The shaping of genetic variation in edge-of-range
569 populations under past and future climate change. *Ecology Letters* 16: 1258–1266.

570 Razgour O., Salicini I., Ibáñez, C., Randi E., Juste J. 2015. Unravelling the evolutionary history and
571 future prospects of endemic species restricted to former glacial refugia. *Molecular Ecology* 24:
572 5267-5283.

573 Riggio J., Jacobson A., Dollar L., Bauer H., Becker M., Dickman A., et al. 2012. The size of savannah
574 Africa: a lion's (*Panthera leo*) view. *Biodiversity and Conservation* 22: 17–35.

575 Schmitz O.J., Hawlena D., Trussell G.C. 2010. Predator control of ecosystem nutrient dynamics. *Ecology*
576 *Letters* 13: 1199–209.

577 Schuette P., Creel S., Christianson D., 2013. Coexistences of African lions, livestock, and people in a
578 landscape with variable human land use and seasonal movement. *Biological Conservation* 157:
579 148-154

580 Schwartz M.W. 2012. Using niche models with climate projections to inform conservation management
581 decisions. *Biological Conservation* 155: 149-156

582 Stanton J.C., Pearson R.G., Horning N., Ersts P., Resit-Akçakaya H. 2012. Combining static and dynamic
583 variables in species distribution models under climate change. *Methods in Ecology and*
584 *Evolution* 3: 349-357

585 Stehfest E., van Vuuren D., Kram T., Bouwman L., Alkemade R., Bakkenes M., et al. 2014. Integrated
586 Assessment of Global Environmental Change with IMAGE 3.0. Model description and policy
587 applications. PBL Netherlands Environmental Assessment Agency, The Hague, Netherlands.

588 Swanson A., Caro T., Davies-Mostert H., Mills M.G.L., Macdonald D.W., Borner M., Masenga E.,
589 Packer C. 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions.
590 *Journal of Animal Ecology* 83: 1418-1427

- 591 Thuiller W., Albert C., Araujo M.B., Berry P.M., Cabeza M., Guisan A., et al. 2008. Predicting global
592 change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology,*
593 *Evolution and Systematics* 9: 137-152
- 594 Van Der Meer E., Moyo M., Rasmussen G.S.A., Fritz H. 2011. An empirical and experimental test of risk
595 and costs of kleptoparasitism for African wild dogs (*Lycaon pictus*) inside and outside a
596 protected area. *Behavioural Ecology* 22: 985-992
- 597 Vanak A.T., Fortin D., Thaker M., Ogden M., Owen C., Greatwood S., Slotow R., et al. 2013. Moving to
598 stay in place: Behavioural mechanisms for coexistence of African large carnivores. *Ecology* 94:
599 2619-2631
- 600 Warren D.L., Glor R.E., Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental
601 niche models. *Ecography* 33: 607-611
- 602 Watson F., Becker M., Milanzi J., Nyirenda M. 2015. Human encroachment into protected area networks
603 in Zambia: implications for large carnivore conservation. *Regional Environmental Change*
604 15:415-429
- 605 Wisz M.S., Pottier J., Kissling W.D., Pellissier L., Lenoir J., Damgaard C.F., et al. 2013. The role of
606 biotic interactions in shaping distributions and realised assemblages of species: implications for
607 species distribution modelling. *Biological Reviews* 88: 15-30
- 608 Wittington-Jones B.M., Parker D.M., Bernard R.T.F., Davies-Mostert H.T. 2014. Habitat selection by
609 transient African wild dogs (*Lycaon pictus*) in northern KwaZulu-Natal, South Africa:
610 Implications for range expansion. *South African Journal of Wildlife Research* 44: 135-147
- 611 Woodroffe R., Ginsberg J.R. 1999. Conserving the African wild dog *Lycaon pictus*. I. Diagnosing and
612 treating causes of decline. *ORYX* 33: 132-142
- 613 Woodroffe R., Sillero-Zubiri C. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species 2012:
614 e.T12436A16711116. <http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T12436A16711116.en>.
615 [Accessed on 7th December 2015].

616 **Acknowledgements**

617 We are grateful to H. Visser, L. Müller and H.H. de Iongh for providing additional species presence
618 records for use in the distribution modelling, and to R. Cooper-Bohannon for providing maps and advice.

619 O. Razgour was funded through a University of Stirling Impact Fellowship and Natural Environmental
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 + 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

627

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.

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%

631

632

633 **Figures**

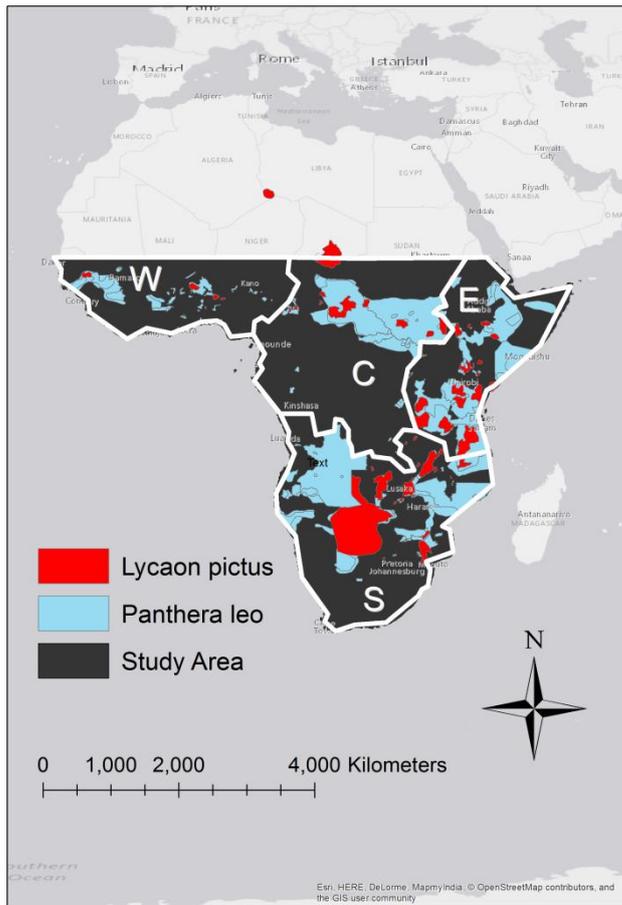
634 **Figure 1** – The selected study area (in black) and species known ranges based on the IUCN RedList
635 (Woodroffe and Sillero-Zubiri, 2012), displayed over an OpenStreetMap base map (ESRI). The
636 geographical regions referred to in the manuscript are marked in white (W=West, C=Central, E=East,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

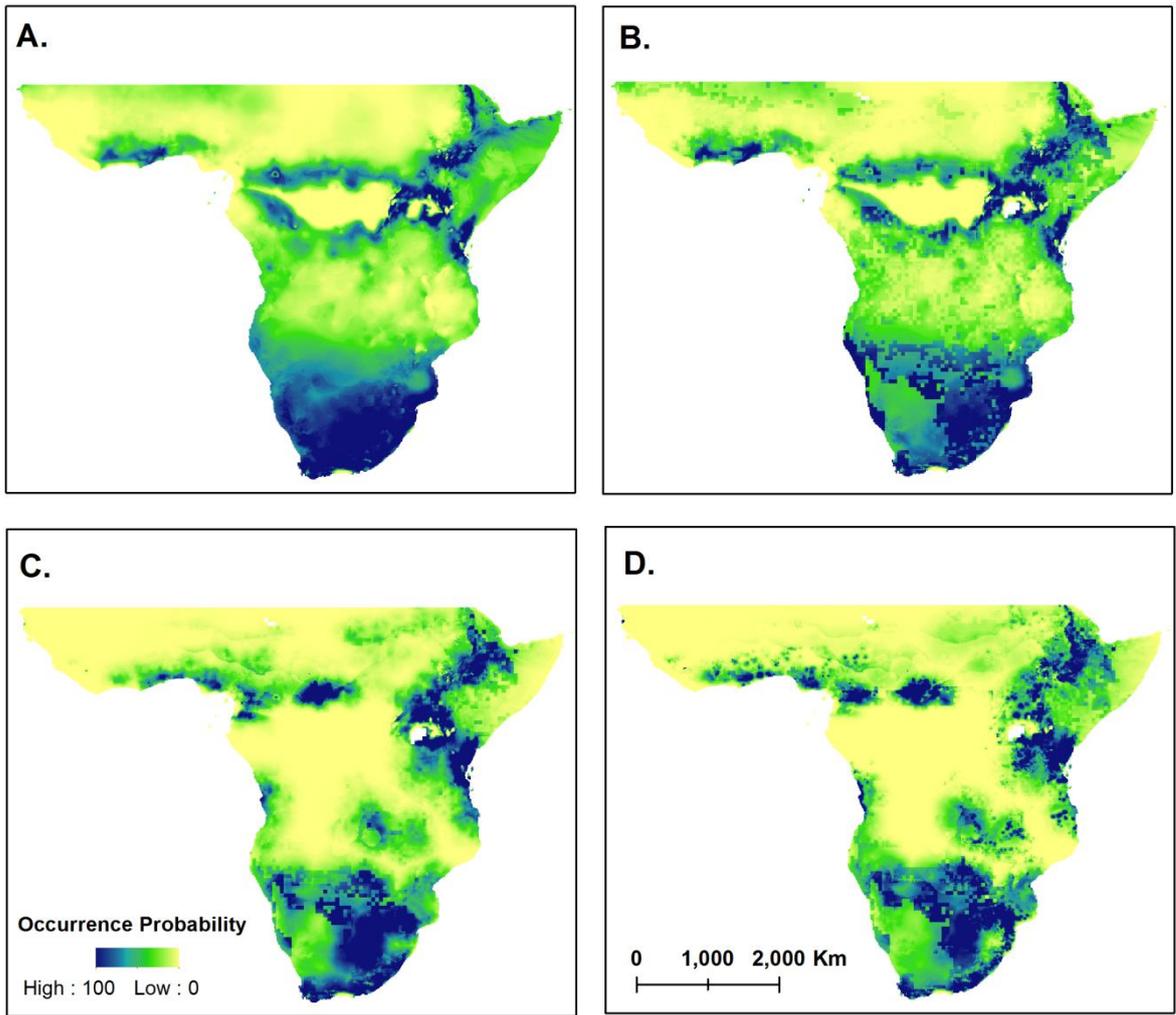
647 **Figure 4** – Predicted change in range overlap between *Lycaon pictus* and *Panthera leo* under present (A)
648 and future (2050; B) conditions.

649 **Figure 1**



650

651



653

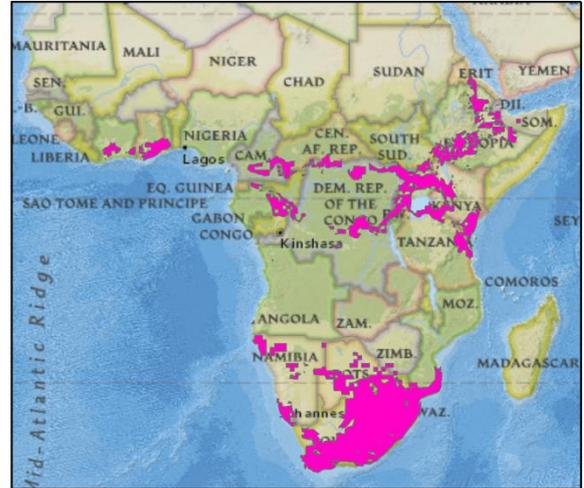
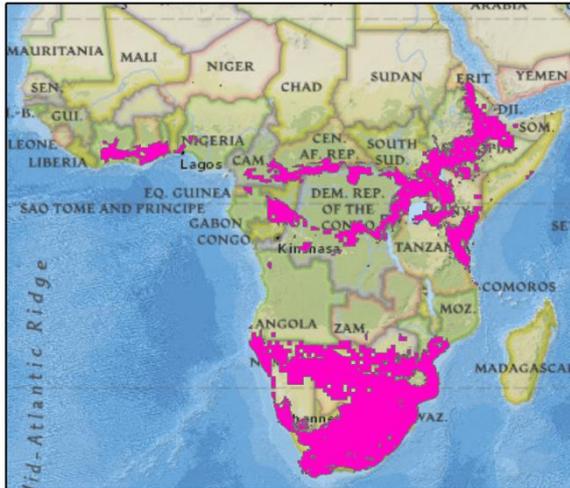
654

Present

Future (2050)

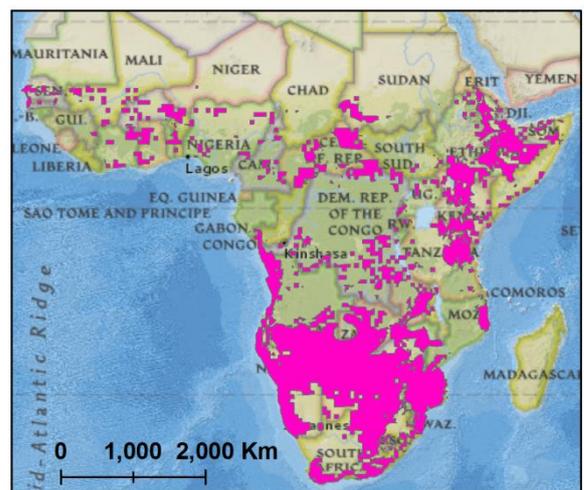
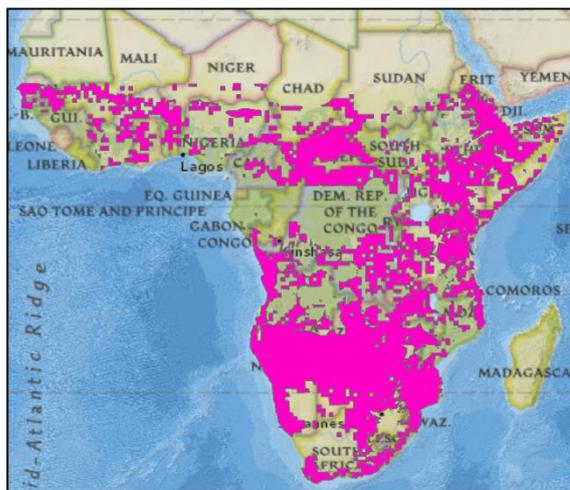
A. *Lycaon pictus*

B. *Lycaon pictus*



C. *Panthera leo*

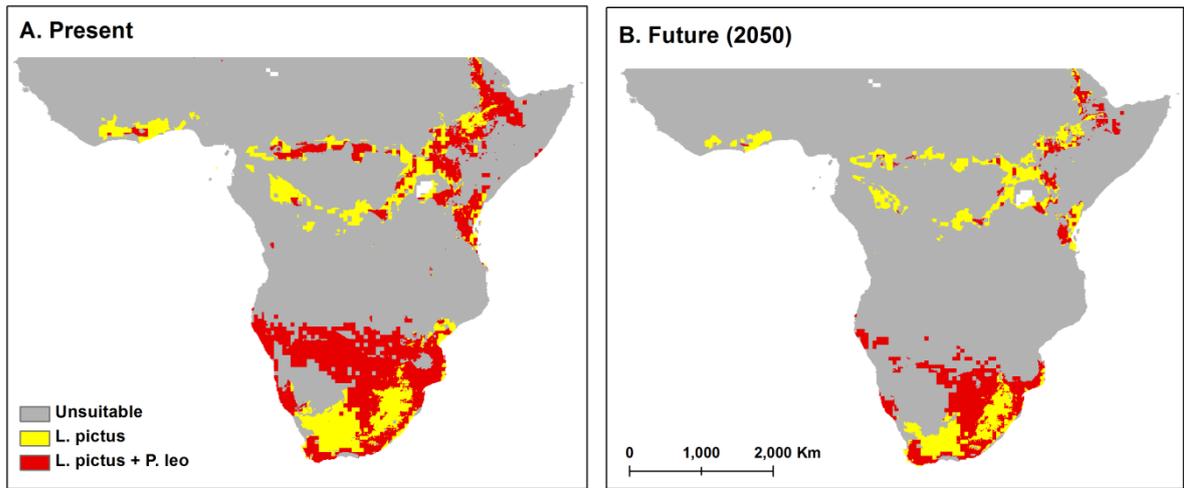
D. *Panthera leo*



656

657

658 **Figure 4**



659