1 Due South: A first assessment of the potential impacts of climate
2 change on Cape vulture occurrence.

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15 Abstract

16 Multiple anthropogenic threats have caused vulture populations to decline globally,

17 with serious ecological and socio-economic implications. The Cape vulture (*Gyps*

18 *coprotheres*) has declined throughout its range in southern Africa, recently being

19 listed as extinct as a breeding species in Namibia. It has been suggested that

20 climate change might have contributed to the decline of Cape vultures in northern

21 parts of the range. To provide a first assessment of the potential impacts of climate

22 change on the occurrence of Cape vultures, a presence-only ecological niche

23 modelling method (Maxent) was used to predict the spatial occurrence patterns of

24 wild-caught vultures fitted with GPS tracking units in northern Namibia and northern

25 South Africa, under current and future climatic conditions. The models showed high

26 predictive power (AUC >0.868±0.006), with precipitation seasonality and other

27 bioclimatic variables identified as the most important variables for predicting Cape

28 vulture presence. Of the area estimated to be suitable for Cape vultures under

29 current conditions, 28-55% was predicted to become unsuitable under future climate

30 conditions, with a pole-ward shift in the mean centre of the range of 151-333 km and

31 significant range loss from the former breeding range in north-central Namibia and

32 the core breeding range in northern South Africa. Expansions of suitable conditions

33 into areas where the species has been historically absent in the south of the range

34 were also predicted. The coverage of predicted suitable areas by protected areas

35 was predicted to decrease from 5.8-7.9% to 2.8-3.8%, suggesting that private land

36 will become increasingly important for Cape vulture conservation.

1. Introduction

Successful efforts to plan and implement conservation strategies in key areas are often reliant on the ability to describe the ecological niche and map the spatial distribution of threatened species to inform their management, ecosystem restoration, reintroduction programs and population viability analysis (Elith *et al.* 2011; Razgour *et al.* 2011; Guillera-Arroita *et al.* 2015). Ecological niche modelling (ENM) or species distribution modelling (SDM) methods estimate the relationship between species presence records at sites and the environmental characteristics of those sites, and are widely used in conservation biology and ecology (Elith *et al.* 2011). Increasingly Global Positioning System (GPS) tracking data provide the species presence records necessary for ENM analyses (Hebblewhite and Haydon 2010) for conservation themed studies on terrestrial (Swanepoel *et al.* 2013; Van Gils *et al.* 2014) and avian species (Jiguet *et al.* 2011; Gschweng *et al.* 2012; Liminana *et al.* 2014). Maxent (Phillips *et al.* 2006) is a common and favoured method for ENM analysis using tracking data because it does not require true absence data and has been shown repeatedly to outperform other presence-only modelling techniques (Elith *et al.* 2006; Hernandez *et al.* 2006). Examples of its successful application with avian tracking data include predicting the extent of suitable wintering habitats for pallid (*Circus macrourus*) and Montagu's (*Circus pygargus*) harriers in sub-Saharan Africa (Liminana *et al.* 2012; Liminana *et al.* 2014), and the response of Eleonora's falcons (*Falco eleonorae*) to environmental change (Gschweng *et al.* 2012).

African vulture populations are declining across the continent due to multiple anthropogenic threats such as poisoning (Ogada *et al.* 2015a), collisions and electrocutions on the expanding power line network (Boshoff *et al.* 2011) and food shortages due to depleted wild ungulate populations and improved livestock husbandry (Mundy *et al.* 1992; Krueger *et al.* 2015; Ogada *et al.* 2015b). The potential consequences of continuing declines are likely to be far reaching due to the essential ecosystem services that vultures provide (e.g. nutrient recycling; limiting

69　the development and spread of disease (Sekercioglu 2006; Moleon *et al.* 2014;

70　Morales-Reyes *et al.* 2015)). However, despite an increasing number of remote

71　tracking studies on African vulture species (Phipps *et al.* 2013a; Spiegel *et al.* 2013;

72　Kendall *et al.* 2014; Krueger *et al.* 2014) to our knowledge there has been no attempt

73　to investigate what drives their spatial distribution using GPS tracking data and

74　multivariate ENM methods.

75　The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is listed as

76　Endangered on the IUCN Red List due to recently estimated population declines of -

77　92% over three generations (48 years), at a median annual rate of -5.1% (Ogada *et*

78　*al.* 2015b; BirdLife International 2016). It is a gregarious cliff-nesting species with a

79　global population estimated at 8,000–10,000 individuals (circa 4,000 breeding pairs)

80　(BirdLife International 2016). The largest remaining breeding colonies are located in

81　the north-eastern provinces of South Africa with smaller, more dispersed colonies in

82　the Maloti-Drakensberg mountains of Lesotho and south-east South Africa

83　(Rushworth and Kruger 2014; Wolter *et al.* 2016). An isolated breeding colony

84　located on the cliffs of the Waterberg Plateau Park in north-central Namibia that

85　numbered 500 Cape vultures in 1940 was reduced to as few as 13 individuals in

86　1985 (Brown 1985) and the species has recently been classified as extinct as a

87　breeding species in the country (BirdLife International 2016). The declines have

88　been mainly attributed to the widespread use of poisons for killing predators in the

89　region and the loss of foraging habitat due to shrub encroachment (Brown 1985;

90　Mundy *et al.* 1992; Bamford *et al.* 2007; Schumann *et al.* 2008; Bamford *et al.* 2009).

91　It has also been suggested that climate change may have played a role in the

92　extinction of Cape vulture colonies in the north of their range since the 1950s due to

93　the increasing temperatures and changing rainfall patterns recorded in the region

94　during that time period (Simmons and Jenkins 2007; IPCC 2014). Southern Africa,

95　and Namibia in particular, is predicted to experience particularly significant changes

96　to climatic conditions (e.g. rising temperatures and altered rainfall patterns (Conway

97　*et al.* 2015; van Wilgen *et al.* 2016)) which are expected to drive pole-wards range

98　shifts and loss of climatically suitable conditions for many species from different taxa

99　(Simmons *et al.* 2004; Thuiller *et al.* 2006b; Midgley and Thuiller 2011; Garcia *et al.*

100　2012). There is evidence to suggest that breeding Cape vultures suffer increased

101　levels of heat stress in higher temperatures and longer sunlight exposures

102 (Chaudhry 2007); rainfall patterns influence vulture breeding success (Bridgeford

103 and Bridgeford 2003; Virani *et al.* 2012); and increased temperatures and carbon

104 dioxide levels enhance woody vegetation cover (Midgley and Bond 2015), inhibiting

105 the visual foraging of vultures by obscuring carcasses (Bamford *et al.* 2009).

106 Simmons and Jenkins (2007) therefore propose that climate change may work in

107 concert with other factors to push Cape vultures away from their northernmost

108 colonies in a southwards direction, and further work is required to investigate the

109 potential impacts of climate change on Cape vulture occurrence (Krueger *et al.*

110 2015).

111 In this study we use Maxent modelling to provide a first description of the spatial

112 niche characteristics for Cape vultures and identify some of the environmental

113 factors driving their occurrence. The presence locations were derived from GPS

114 tracking data from wild caught vultures from northern South Africa (Phipps *et al.*

115 2013b) and from some of the last remaining Cape vultures in Namibia (Bamford *et*

116 *al.* 2007). We investigate the potential influence of climate change on the extent of

117 areas predicted to be currently suitable by projecting the models onto future

118 bioclimatic conditions. We compare results from models using only data from South

119 African tagged vultures with models from data from all vultures to assess whether

120 conditions in north-central Namibia are predicted to be suitable for Cape vultures

121 under current and future climate scenarios. We also evaluate the coverage provided

122 by protected areas to areas modelled to be suitable for Cape vultures under current

123 and future conditions as species turnover in protected areas is expected to be high in

124 the region (Hole *et al.* 2009). The intention of this study is to provide a first

125 description of the spatial niche of a sample of Cape vultures from the core breeding

126 range of the species and to assess whether vulture occurrence patterns might be

127 influenced by global climate change.

128 **2. Methods**

129 *2.1. Modelling method and study area*

130 The presence-only method Maxent (Phillips *et al.* 2006) was used to model the

131 ecological niche of the Cape vulture as it does not require true absence data (Elith *et*

132 *al.* 2011) and has been used previously with avian tracking data obtained from a

133 small number of individuals (Gschweng *et al.* 2012; Liminana *et al.* 2012; Liminana

134 *et al.* 2014). The geographical area used for ecological niche modelling was
135 delineated by the national borders of South Africa, Lesotho, Swaziland, Zimbabwe,
136 Botswana and Namibia, to correspond with the historical distribution of the Cape
137 vulture (Mundy *et al.* 1992; BirdLife International 2016).

138 *2.2. GPS tracking and presence data*
139 Presence locations were derived from two studies that fitted GPS tracking units to
140 wild-caught Cape vultures using walk-in cage traps (Bamford *et al.* 2007; Phipps *et*
141 *al.* 2013b). The first capture site was located on a private livestock and game farm in
142 the Waterberg region of north east Namibia (20°15'54"S, 17°03'53"E) while the
143 second was on a private wildlife reserve in the North West Province of South Africa
144 (25°13'S, 27 $^\circ$18'E). Vultures captured in Namibia were fitted with solar-powered
145 Argos/GPS PTT-100 tracking units made by Microwave Telemetry Inc. (Columbia,
146 Maryland) programmed to record GPS locations every hour from 06:00 to 21:00
147 CAT (Bamford *et al.* 2007). The vultures captured in South Africa were fitted with
148 battery-powered Hawk105 GPS-GSM tracking units programmed to record GPS
149 locations up to four times per day at 07:00, 11:00, 13:00 and 15:00 CAT (Phipps *et*
150 *al.* 2013b). Tracking units were fitted to vultures with Teflon$^\circledR$ ribbon backpack-style
151 harnesses and GPS locations were accurate to within 10 m. Data were derived from
152 a total of five adult and four immature Cape vultures tagged in South Africa and five
153 adults tagged in Namibia. The nine South African tagged vultures were tracked from
154 2009 to 2011 for 31-558 days (median tracking period = 300 days; median number of
155 GPS locations = 922, range = 84-1860), and the five vultures from Namibia were
156 tracked from 2004 to 2009 for 57-1656 days (median tracking period = 1231 days;
157 median number of GPS locations = 15 447, range = 654-19400).

158 Two datasets of presence locations were selected for modelling purposes. Firstly,
159 one dataset consisted of GPS locations only obtained from the nine South African
160 tagged vultures, while the second consisted of GPS locations from all 14 vultures.
161 This was done to compare results based on data from only South African tagged
162 birds (i.e. captured in the "core" of the species' breeding range (Mundy *et al.* 1992;
163 BirdLife International 2016)) to those that included presence locations from Namibia
164 where the species formerly bred but is now considered extinct as a breeding species
165 (Brown 1985; BirdLife International 2016). This provided an indication of the
166 suitability of environmental conditions in northern Namibia compared to the rest of

167 the study area and whether or not the region was predicted to be more or less

168 affected by climate change compared to more southern areas during subsequent

169 analyses.

170 Spatial preparation of GPS location and environmental variable data was performed

171 in SDMtoolbox v1.1b (Brown 2014) in ArcMap (ESRI 2014) with all data projected to

172 the Africa Albers Equal Area Conic coordinate system. For both presence datasets

173 only stationary (<10 kmh^{-1}) GPS locations were selected to more accurately

174 represent actual use of a given area. The Namibian tracking dataset was filtered

175 further by only including GPS locations recorded every two hours from 09:00 to

176 17:00 CAT to reduce spatial autocorrelation and to correspond with the diurnal

177 activity patterns of the vultures (Bamford *et al.* 2007). To further reduce spatial

178 autocorrelation, which can influence species distribution model performance (Boria

179 *et al.* 2014), the presence locations for each individual vulture were filtered by using

180 the *spatially rarefy occurrence data* tool in SDMtoolbox v1.1b (Brown 2014) in

181 ArcMap (ESRI 2014) to reduce clusters of presence locations to a single presence

182 location within a Euclidean distance of 1 km. In order to reduce the influence of the

183 disparity in tracking periods, and therefore the number of GPS locations per

184 individual (Gschweng *et al.* 2012; Liminana *et al.* 2014), the mean number of

185 stationary GPS locations rarefied by 1 km for the nine South African tagged vultures

186 was calculated (mean±SD = 238±151 GPS locations per individual) and used to

187 select a random subsample of 238 GPS locations for all individuals for which more

188 than 238 stationary rarefied GPS locations were available using statistical software R

189 v3.1.1 (R Core Team 2014). The maximum number of GPS locations per vulture was

190 therefore limited to 238 and all stationary rarefied GPS locations were retained for

191 vultures with less than 238 stationary rarefied GPS locations. Finally, the GPS

192 locations for all individuals were merged into one shapefile and further spatially

193 rarefied to a Euclidean distance of 1km. The two final presence location datasets

194 consisted of 1437 presence locations for the South African tagged individuals and

195 2123 presence locations for the South African and Namibian tagged vultures

196 combined (i.e. 686 presence locations for the five Namibian vultures; Fig. 1a).

197 Capture and tagging procedures were approved by the ethical review committee of

198 the School of Animal, Rural and Environmental Science, Nottingham Trent

199 University, and permits were granted by the Department of Agriculture,

200   Conservation, Environment and Rural Development, North West Provincial

201   Government, Republic of South Africa (Permit: 000085 NW-09) and the Namibian

202   Ministry of Environment and Tourism (Permit: 1578/2004-2005). All procedures were

203   carried out by South African Bird Ringing Unit permit holders.

204   *2.3. Environmental variables*

205   Only environmental variables with a pairwise Pearson's correlation coefficient of less

206   than 0.7 (assessed using SDMtoolbox v1.1b (Brown 2014)) were included in the

207   modelling process to reduce multi-collinearity effects (Phillips and Dudik 2008).

208   Environmental variables were subsequently selected based on prior knowledge of

209   their ecological relevance to Cape vultures and their contribution to preliminary

210   models in an effort to achieve parsimony to reduce the risk of over-fitting (Anderson

211   and Gonzalez 2011; Van Gils *et al.* 2014). The models included a total of 14

212   environmental variables (Table 1, Table A1) at a spatial resolution of 30 arc-seconds

213   (approximately 1 km^2 at the equator): seven bioclimatic variables from the WorldClim

214   database (http://www.worldclim.org/; (Hijmans et al. 2005)); two topographic

215   variables (elevation and slope) derived from the digital elevation model (DEM) data

216   from the WorldClim database; Normalised Difference Vegetation Index (NDVI) data

217   for August derived from the SPOT (Satellite Pour l'Observation de la Terre;

218   http://www.cnes.fr/web/CNES-en/1415-spot.php) program; the Food and Agriculture

219   Organisation (FAO) global cattle density dataset (FAOcattle05; http://www.fao.org;

220   (Robinson et al. 2007)); the FAO ruminant production systems dataset (Robinson et

221   al. 2011)); Global Land Cover 2000 (Mayaux et al. 2004); and the World Wildlife

222   Fund (WWF) terrestrial ecoregions of the world dataset classified by ecoregion ID

223   code (http://www.worldwildlife.org/biome-categories/terrestrial-ecoregions; (Olson et

224   al. 2001)). Similar variables have previously performed well when modelling bird

225   distributions (Barbet-Massin *et al.* 2009; Jiguet *et al.* 2011; Liminana *et al.* 2012;

226   Liminana *et al.* 2014) and are known to influence vulture flight patterns (e.g.

227   isothermality; (Pennycuick 1972; Harel *et al.* 2016)) and the availability of carrion due

228   to seasonal changes in ungulate mortality driven by fluctuations in vegetation

229   productivity (Houston 1974b; Mduma *et al.* 1999; Owen-Smith *et al.* 2005; Ogutu *et*

230   *al.* 2008). More detailed information on the selection of environment variables can be

231   found in the "Environmental Data" section in Supporting Information.

232 For projections to future climatic conditions the current Bioclim variables were
233 replaced with the corresponding Bioclim variables for the year 2050 from the
234 WorldClim database from the HadGEM-AO model under emissions scenario RCP
235 8.5 which is a "worst case" scenario that predicts increasing greenhouse gas
236 emissions and a likely global mean temperature increase of $1.4 - 2.6^{\circ}C$ between
237 2046 and 2065 (Riahi *et al.* 2007). In the absence of credible projections to our
238 knowledge, other environmental variables remained the same for projected models
239 as for the current models. We acknowledge this is unlikely given projected climate,
240 land use and socio-economic changes.

241 *2.4. Ecological niche modelling procedure*
242 Models were run using default settings in Maxent version 3.3.3 (Phillips *et al.* 2006)
243 apart from the maximum number of iterations which was set at 5000 to achieve
244 algorithm convergence (Elith *et al.* 2011; Kassara *et al.* 2013). Ten replicate models
245 were run each using repeated random subsampling of 75% of the presence locations
246 to train the model with the remaining 25% used to evaluate its predictive
247 performance (i.e. test dataset). Results are presented as the mean and standard
248 deviations of the ten replicate models. Two metrics were used to evaluate model
249 performance (Elith and Graham 2009). Firstly, the area under the curve (AUC) of the
250 receiver operating characteristics (ROC) was used to measure the model probability
251 of correctly distinguishing presence from random locations, with values of 0.5
252 indicating models that predict no better than random and values greater than 0.75 for
253 models with high model discrimination ability (Phillips *et al.* 2006; Elith *et al.* 2011).
254 The second metric, regularized training gain, describes how well the model
255 prediction fits the presence data compared to a uniform distribution, with the
256 exponential of the model gain indicating the sample likelihood compared to random
257 background pixels (Phillips *et al.* 2006; Gormley *et al.* 2011).

258 Variable importance was assessed using two heuristic tests (percent contribution
259 and permutation importance) and the jacknife procedure in Maxent. Percent
260 contribution was calculated as the proportional contribution of each variable to the
261 model training gain which is dependent on the path of the Maxent algorithm (Phillips
262 *et al.* 2006). The permutation importance metric is independent of the algorithm path
263 and represents the influence of the given variable on the training AUC value,
264 normalized to percentages (Phillips *et al.* 2006). For the jacknife tests variables were

265 successively omitted and then used in isolation to measure their relative and

266 absolute contribution to model gain, providing a measure of their explanatory power

267 when considered alone (Elith *et al.* 2011; Gschweng *et al.* 2012).

2.5. Assessment of environmental suitability and impact of climate change

269 The logistic output from the Maxent model was used to display the spatial predictions

270 of the probability of Cape vulture presence across the study area with values ranging

271 from 0 to 1 (Phillips and Dudik 2008). To classify the model predictions into areas of

272 binary suitability (1) and unsuitability (0) the mean (0.31) of the maximum training

273 sensitivity plus specificity logistic threshold (*MaxTSS*) for the model with only South

274 African tagged vulture presences (*MaxTSS* = 0.28) and the model with both

275 presence datasets (*MaxTSS* = 0.33) was used. The *MaxTSS* threshold is

276 independent of prevalence of presence locations and is recommended for use with

277 presence only data as an objective method of binary suitability threshold selection

278 (Jiguet *et al.* 2011; Liu *et al.* 2013). Binary maps of suitability were created using this

279 method for both current and future (for the year 2050) climatic conditions for the two

280 different presence datasets on which the models were based (i.e. *Model_SA* =

281 presence locations from South African tagged vultures; *Model_NamSA* = presence

282 locations from both South African and Namibian tagged vultures). Subsequently the

283 areas predicted to be unsuitable and suitable were compared for each model

284 separately under the current and future environmental conditions. This was done in

285 ArcMap to produce a raster dataset with areas predicted to be unsuitable in both

286 current and future conditions; suitable under current but not future environmental

287 conditions (range contraction); unsuitable under current conditions but suitable under

288 future conditions (range expansion); and suitable under both current and future

289 conditions (stable range). The distance between the mean centres of the extent of

290 the suitable areas under current and future conditions was calculated in ArcMap to

291 quantify the directional range shift from current to future conditions.

2.6. Evaluation of protected area coverage

293 To assess the level of protection afforded to areas predicted as suitable for Cape

294 vultures based on the binary suitability maps, the number of suitable raster cells

295 located within nationally and internationally designated protected areas in the 2015

296 World Database on Protected Areas (IUCN and UNEP-WCMC 2015) were counted

297 for current and future models in ArcMap (Liminana *et al.* 2012; Swanepoel *et al.*
298 2013; Liminana *et al.* 2014).

299 **3. Results**

300 *3.1. Ecological niche model description and variable importance*

301 The model constructed with the presence locations only from the South African
302 tagged birds (Model_SA) and the model constructed with presence locations from
303 South African and Namibian tagged birds (Model_NamSA) showed good predictive
304 power based on mean AUC values of the 10 replicate runs (Model_SA AUC =
305 0.886±0.009; Model_NamSA AUC = 0.868±0.006), although the regularized training
306 gain was lower for Model_NamSA (0.906±0.009) compared to Model_SA
307 (1.084±0.009).

308 Model_SA classed 15.08% of the study area (460,801 km^2) as suitable for Cape
309 vultures under current environmental conditions, while Model_NamSA classed
310 16.09% (491,655 km^2) of the area as suitable. The majority of the suitable area
311 predicted by both models consisted of an almost continuous area in northern South
312 Africa across most of the North West Province, the western half of the Limpopo
313 Province and into south-east Botswana, corresponding with the extent of the known
314 distribution for the species (Fig. 1b and c; Fig. A1). The suitable area also extended
315 into the north-east of the Northern Cape Province and the western part of the Free
316 State. A relatively narrow area of suitability was predicted along the south- and
317 north-eastern edges of the Drakensberg escarpment bordering Lesotho in the north-
318 eastern Eastern Cape and western edge of KwaZulu-Natal Provinces. This area was
319 separated from the main region of suitability by an area of unsuitability estimated to
320 extend in a south-west to north-easterly direction, almost 700 km long by 200 km
321 wide across southern Gauteng, southern Free State and the south-west of
322 Mpumulanga Province (Fig. 1b and c). In addition, Model_NamSA predicted
323 environmental suitability in an isolated area in north-central Namibia extending up to
324 300 km south and east of the Waterberg Mountains (Fig. 1c). Outlying areas of
325 suitability were predicted in south-east Namibia, north-west Northern Cape and
326 south-east Zimbabwe for Model_SA (Fig. 1b); and north-west Zimbabwe and an
327 isolated area across the Namibia-Botswana Trans-Kalahari border for
328 Model_NamSA (Fig. 1c).

329　According to the heuristic tests of variable importance bioclimatic variables were the

330　most influential to model predictions in terms of percent contribution and permutation

331　importance (Fig. A2), with precipitation seasonality (Bio_15) contributing

332　29.88±2.14% (35.98±2.72% permutation importance) to Model_SA and five

333　bioclimatic variables ($Bio\_2, 12, 6, 3$ and 1 in descending order) collectively

334　contributing 73.70% to Model_NamSA (Fig. A2). The four variables that contributed

335　the most to Model_SA ($Bio\_15, 6, 12$ and 19 in descending order) collectively

336　contributed 70.44% to the model. Elevation (*alt*) was also a relatively important

337　variable with a permutation importance of 20.99% for Model_NamSA and 10.08% for

338　Model_SA. The jacknife tests for variable importance identified precipitation

339　seasonality (Bio_15) as the most important variable for both models, followed by

340　precipitation of the coldest quarter (Bio_19), minimum temperature of the coldest

341　week (Bio_6) and WWF ecoregion ID for Model_SA (Fig. A2). WWF ecoregion ID

342　was also identified as an important variable for Model_NamSA, followed by altitude,

343　minimum temperature of the coldest week (Bio_6) and NDVI in August (Fig. A2).

344　According to the jacknife tests exclusion of the variables from the models did not

345　identify any obvious single variable that contained information that was lacking in the

346　other variables, although the omission of precipitation seasonality (Bio_15) and

347　isothermality (Bio_3) resulted in the greatest decrease in gain for Model_SA and

348　Model_NamSA, respectively (Fig. A2).

349　The average variable values for raster cells predicted to be suitable for Cape

350　vultures were similar for Model_SA and Model_NamSA (Table 1). The elevational

351　range of cells predicted to be suitable for Cape vulture occurrence under current

352　conditions for both models was 517 – 3 308 m·asl compared to 389 – 3 148 m·asl

353　under future conditions. For all models, cells predicted to be suitable for Cape vulture

354　occurrence tended to consist, on average (median and mode), of "livestock-only

355　ruminant production systems in arid areas" with mean (±SE) cattle densities from

356　9.34±0.014 cattle·km^{-1} (Model_NamSA current) to 13.31±0.023 cattle·km^{-1}

357　(Model_NamSA 2050), in areas of "open grassland with sparse shrubs" land-cover in

358　the Highveld grasslands or Kalahari xeric savannah ecoregions (Table 1).

359　*3.2. Projected extent of predicted environmental suitability*

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360   Of the 460,801 km^2 predicted by Model_SA to be suitable for Cape vultures under

361   current conditions, 28% was predicted to become unsuitable in 2050 with a pole-

362   ward 151 km shift of the mean centre of the suitable area (Fig. 1b). However, under

363   future conditions the overall suitable area was predicted to increase from 15% to

364   19% (594,964 km^2) of the study area, of which 44% (264,070 km^2) extended into

365   areas predicted to be unsuitable in current conditions (Fig. 1b). For Model_NamSA a

366   greater degree of current suitable range loss was predicted, with 55% of the 491,655

367   km^2 current suitable range predicted to become unsuitable in 2050, with a pole-ward

368   333 km shift of the mean centre of the suitable area (Fig. 1c). 56% (284,662 km^2) of

369   the area predicted to be suitable in 2050 was predicted to be unsuitable in current

370   conditions, resulting in a relatively small increase in the area predicted to be suitable

371   across the study area to 504,911 km^2 (Fig. 1c). Both models predicted that the

372   largest area of range contraction would be in the western half of the Limpopo

373   Province, South Africa, and south-east Botswana (Fig. 1b and c). Almost the whole

374   area in north-central Namibia predicted to be suitable under current conditions by

375   Model_NamSA was predicted to become unsuitable under climatic conditions in

376   2050 (Fig. 1c; Fig. A1). The mean elevation (*alt*) for areas predicted to be suitable

377   increased by 124 m and 171 m for Model_SA and Model_NamSA, respectively

378   (Table 1).

379   *3.3 Protected area coverage under current and projected suitability*

380   Of the area predicted by Model_SA to be suitable for Cape vultures, 5.85% (26 961

381   km^2) and 3.79% (22 560 km^2) was included within protected areas under current and

382   future conditions, respectively. The protected areas covering more than 1,000 km^2 of

383   suitable area under current conditions were the Waterberg Biosphere Reserve (BR)

384   in Limpopo Province, South Africa, the Drakensberg World Heritage Site (WHS), and

385   the Central Kalahari Game Reserve (GR) in south-east Botswana, whereas under

386   future conditions only the Kalahari-Gemsbok National Park (NP) and the

387   Drakensberg WHS covered more than 1,000 km^2. For Model_NamSA, 7.91%

388   (38,874 km^2) and 2.77% (13,963 km^2) of the predicted suitable area was included

389   within protected areas under current and future conditions, respectively. The

390   protected areas covering more than 1,000 km^2 of suitable area under current

391   conditions were several conservancies in north-central Namibia, the Waterberg BR

392   in Limpopo Province, South Africa, and the Central Kalahari GR in south-east

393 Botswana. Under future conditions only the Drakensberg WHS and the Waterberg
394 BR in Limpopo Province, South Africa, covered more than 1000 km^2 of suitable area.

395 **4. Discussion**

396 This study provides a first description of the environmental characteristics of the
397 spatial niche occupied by the Cape vulture using a presence-only ENM method
398 based on GPS tracking locations from vultures caught from the wild in north-central
399 Namibia and north-central South Africa. As with previous ENM studies on raptor
400 species the most important variables determining the limits of predicted suitability
401 were bioclimatic variables, with precipitation seasonality (i.e. variation in monthly
402 precipitation totals across the course of the year (Table A1)) consistently identified
403 as one of the most influential variables (Gschweng *et al.* 2012; Liminana *et al.* 2012).
404 The areas predicted to be suitable for Cape vultures by both models broadly
405 corresponded with the known current and historical distribution of the species, with a
406 core range in the highveld and bushveld of the northern provinces of South Africa
407 and a secondary region of suitability in the more mountainous south-east of the
408 country, mainly along the Maloti-Drakensberg escarpment (Mundy *et al.* 1992;
409 BirdLife International 2016). The area of suitability also extended beyond the current
410 western boundary of the recognised species distribution range, which has been
411 linked to the relatively recent construction of power lines in an area otherwise devoid
412 of suitable roost sites (Phipps *et al.* 2013b).

413 A first estimate of the potential impact of climate change on the distribution of
414 suitable areas for Cape vultures predicted a pole-ward shift in suitable conditions
415 away from their core breeding and foraging range in northern South Africa, which
416 conforms with projected patterns of bird species' responses to climate change in the
417 region (Simmons *et al.* 2004; Hole *et al.* 2009). The model that included the
418 presence locations from the vultures tagged in Namibia predicted that the majority of
419 an isolated area of suitable conditions centred approximately on the former breeding
420 colony in the Waterberg region would become unsuitable under future (2050)
421 climatic conditions. In proportion to the regional coverage of protected areas in
422 southern Africa (circa 23% of land area, excluding Mozambique; circa 9% of land
423 area for South Africa, Lesotho and Swaziland (IUCN and UNEP-WCMC 2015)), the
424 area predicted to be suitable for Cape vultures located within protected areas (5.85%

425 of suitable area for the model based only on data from South African tagged

426 vultures) was small and predicted to decrease under future conditions.

4.1. Influence of environmental variables on predicted probability of presence

428 Overall, bioclimatic variables, and precipitation seasonality in particular, were the

429 most influential in both models, which is consistent with previous studies that used

430 GPS tracking data to model the ecological niche of raptors (Gschweng *et al.* 2012;

431 Liminana *et al.* 2012). Vegetation production is dependent on climatic conditions and

432 precipitation patterns determine forage abundance and quality, and subsequently

433 nutrition-related mortality rates for ungulates (Boone *et al.* 2006; Ogutu *et al.* 2008;

434 Chamaille-Jammes and Fritz 2009). Vulture movement patterns have been shown to

435 be closely associated with seasonal ungulate mortality rates driven by seasonal

436 changes in vegetation productivity indicated by changes in NDVI, with tracked

437 vultures preferring to forage in areas with higher ungulate mortality during the dry

438 season in the Masai Mara, Kenya (Kendall *et al.* 2014). NDVI in August was

439 identified as the most important variable in the preliminary model which included only

440 the twelve monthly NDVI variables, as well as for both models including all variables.

441 As August is one of the coldest and driest months in southern Africa and mortality of

442 both wild and domestic ungulates can be relatively high during that time as a

443 consequence of nutritional stress (Owen-Smith *et al.* 2005; Mapiye *et al.* 2009), it is

444 likely that the models reflect the influence of seasonal vegetation production on Cape

445 vulture occurrence by affecting the availability of carrion. Correspondingly, the

446 probability of Cape vulture presence was highest in areas with very low levels of

447 precipitation during the coldest quarter (*Bio_19*; Fig. A3b) and temperatures of 2°C

448 to 5°C in the coldest week (*Bio_6*; Fig. A3c), which would result in seasonal periods

449 of low grass productivity and potentially higher ungulate mortality rates (Owen-Smith

450 2008). These results suggest that bioclimatic factors might play a role in driving

451 Cape vulture occurrence and movement patterns, most likely through climatic effects

452 on vegetation production which directly influences the availability of food in the form

453 of ungulate carrion, as reported for vultures in Kenya (Kendall *et al.* 2014). This

454 provides a partial explanation (together with the availability of cliff nesting sites) for

455 why the core breeding and foraging ranges of the species are located in the northern

456 provinces of South Africa which are characterised by distinct wet summer (October –

457 April) and dry winter (May – September) seasons (Benson *et al.* 1990; Mundy *et al.*

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458   1992; Borello and Borello 2002), as Cape vultures and other *Gyps* species tend to

459   coincide their breeding seasons with the highest availability of ungulate carrion in the

460   dry season (Houston 1974b; Piper *et al.* 1999; Virani *et al.* 2010; Virani *et al.* 2012).

461   This is consistent with previous studies that have found an inverse relationship

462   between vulture breeding success and rainfall in the previous year due to reduced

463   ungulate carrion availability (Bridgeford and Bridgeford 2003; Virani *et al.* 2012).

464   As large soaring fliers, vultures are reliant on suitable climatic conditions to provide

465   sufficient air currents and thermals to allow them to cover the large distances

466   required to locate their naturally ephemeral food source and it has been suggested

467   that high rainfall and adverse weather conditions limit their ability to do so

468   (Pennycuick 1972; Lambertucci and Ruggiero 2013; Harel *et al.* 2016). The influence

469   of local climatic factors such as temperature range and precipitation in determining

470   the occurrence of large soaring birds has been shown for the Andean condor (*Vultur*

471   *gryphus*), which should, according to a modelling study, prefer roost sites on

472   climatically stable cliffs in areas of low rainfall (Lambertucci and Ruggiero 2013). The

473   importance of isothermality (a measure of diurnal and annual temperature ranges) in

474   both models (*Bio_3*; Fig. A3f) and the higher probabilities of occurrence in areas with

475   moderate seasonal rainfall, are consistent with this and possibly reflect the influence

476   of meteorological variables on the local flying conditions for large vultures which tend

477   to require strong up-draughts and drier conditions (Shepard and Lambertucci 2013;

478   Harel *et al.* 2016).

479   African vultures locate carcasses by sight alone (Houston 1974a) and it has been

480   shown that high tree densities reduce their ability to locate and land at carcasses,

481   decreasing their foraging efficiency (Schultz 2007; Bamford *et al.* 2009). The results

482   from this study provide further evidence that vegetation and habitat characteristics

483   influence vulture movement and occurrence patterns. WWF ecoregion ID was

484   identified as an important variable for both models, with higher probabilities of Cape

485   vulture presence in habitats characterised by relatively limited tree density and more

486   open habitats (e.g. highveld grassland and southern African bushveld (Olson *et al.*

487   2001)). In addition, the most prevalent land cover type in the modelled suitable areas

488   was open grassland with sparse shrubs which is also defined by relatively low tree

489   densities (Table 1 (Mayaux *et al.* 2004)). These results correspond with previous

490   descriptions of suitable Cape vulture habitat (Mundy *et al.* 1992) and support

491 suggestions that they avoid heavily wooded areas and might be susceptible to the
492 increasing rate and extent of bush encroachment in southern Africa (Schultz 2007;
493 Bamford *et al.* 2009).

494 Although variables related to land use and farming practices (FAO ruminant
495 production systems; Global Land Cover 2000; FAO cattle density for 2005) were not
496 identified as particularly important variables for either model, relatively high
497 probabilities of presence were predicted in livestock-only systems compared to more
498 arable-dominated landscapes (Fig. A4b), with an average cattle density of
499 approximately 10 cattle km^{-2} in suitable areas and a sharp decrease in probability of
500 presence predicted above approximately 20 cattle km^{-2} (Fig. A4c). This supports
501 suggestions that ungulate mortality rather than abundance is a main driver of vulture
502 presence (Kendall *et al.* 2014), particularly as more intensive farming systems
503 remove carcasses more frequently, reducing food availability for vultures (Murn and
504 Anderson 2008; Margalida *et al.* 2014). These patterns are also consistent with
505 observations that Cape vultures often utilise commercial farmland in addition to more
506 extensive systems to exploit all sources of available carrion, including domestic
507 livestock, as well as wild ungulates (Benson *et al.* 2004; Murn and Anderson 2008;
508 Phipps *et al.* 2013b). Consequently, food availability is likely to remain the primary
509 factor in determining vulture occurrence patterns, and it is possible that the growing
510 number of supplementary feeding sites for vultures in southern Africa will influence
511 their movement patterns (Phipps *et al.* 2013a) and possibly assist them to adapt to
512 fluctuating ungulate mortality patterns caused by the changing climate (Cortés-
513 Avizanda *et al.* 2016).

514 *4.2. Projected influence of climate change*

515 The pole-ward shifts and increase in mean altitude of areas predicted to be suitable
516 for Cape vultures in 2050 by both models correspond with previous studies that have
517 predicted similar responses to changing climatic conditions in bird species in
518 southern Africa (Simmons *et al.* 2004; Hole *et al.* 2009; Willis *et al.* 2009; BirdLife
519 International and Durham University 2015). Although the model that used presence
520 locations from Namibian tagged vultures predicted an area of suitability in the north-
521 central region of the country (Fig. 1c and A1c), the model that only used presence
522 locations from South African tagged vultures predicted a very low probability of

523   presence in the same area (Fig. 1b and A1a). This indicates that bioclimatic

524   conditions are very different in north-central Namibia compared to the majority of the

525   predicted suitable area in South Africa and south-east Botswana (Williams *et al.*

526   2007). Under future conditions the area modelled to be suitable in north-central

527   Namibia was predicted to contract away from its current extent in a southwards

528   direction more than 170 km from the former Cape vulture breeding colony on the

529   cliffs of the Waterberg Plateau (Fig. 1c). This is consistent with previous studies that

530   predict that northern Namibia is likely to be particularly vulnerable to the effects of

531   climate change as current climatic conditions shift pole-wards or even disappear,

532   causing high rates of range loss for a high number of species from different taxa

533   (Thuiller *et al.* 2006a; Thuiller *et al.* 2006b; Williams *et al.* 2007; Garcia *et al.* 2012).

534   Significant range loss was also predicted by both models in the current core

535   breeding range of Cape vultures in northern South Africa and south-east Botswana

536   (Fig. 1b and c), areas which have previously been predicted to undergo high levels

537   of bird and mammal species turnover and range loss driven by climate change

538   (Thuiller *et al.* 2006a; Hole *et al.* 2009). These modelled patterns of range

539   contraction support the suggestion that the most northernmost Cape vulture

540   breeding colonies could be at risk of becoming climatically unsuitable for the species

541   in the future, and that climate change might have already played a role in the

542   extinction of the only breeding colony in northern Namibia (Simmons and Jenkins

543   2007). Correspondingly, recent colony surveys indicate that while several peripheral,

544   northern colonies have been abandoned, the core breeding population in the

545   Magaliesberg mountains remains stable, where an increase in supplementary

546   carrion at vulture feeding sites might have led to higher local survival rates and

547   recruitment from more peripheral colonies (Wolter *et al.* 2016), potentially mitigating

548   any adverse impacts of climate change. The influence and interaction of these

549   factors requires further investigation, however.

550   In contrast to the loss of suitable areas in the north of the modelled range, an

551   increase in the overall extent of the suitable area was predicted by both models,

552   largely as a result of a southwards range expansion into the highveld grassland of

553   the Free State and south-west Mpumalanga Provinces (Fig. 1b and c). This region is

554   considered to be outside the historical distribution of the Cape vulture partly due to

555   the relatively long distances from major breeding colonies but also due to the

556 relatively low abundance of trees for roosting and perching after long-term
557 overgrazing suppression and habitat degradation (Mundy *et al.* 1992; Low and
558 Rebelo 1998; Olson *et al.* 2001). Therefore, although large bodied species, such as
559 Cape vultures, that exhibit evidence of nomadic-like movements (Phipps *et al.*
560 2013a; Phipps *et al.* 2013b) are predicted to be more capable of dispersing to
561 suitable areas under future climate change scenarios (Simmons *et al.* 2004; Dodge
562 *et al.* 2014), dispersal capabilities were not considered in this study and so any
563 predicted range expansions should be considered with caution, particularly as there
564 are no active breeding colonies in the area and other factors such as land use
565 change were not accounted for (Guisan and Thuiller 2005). Nevertheless, fluctuating
566 carrion availability regularly forces vultures to shift their movement patterns (Kendall
567 *et al.* 2014), and they even forage beyond their historical distribution by perching on
568 newly constructed power line structures in areas previously devoid of natural
569 perches (Phipps *et al.* 2013b), indicating that they might show a degree of plasticity
570 in their movement patterns in response to future climate change (Simmons *et al.*
571 2004; Dodge *et al.* 2014).

572 *4.3. The current and future role of protected areas*

573 The limited coverage (<6% for Model_SA) of the modelled suitable Cape vulture
574 range by protected areas under current climatic conditions reflects the distribution of
575 relatively small, isolated protected areas in the majority of South Africa, particularly
576 away from the east of the country, that cover just over 9% of the land surface (Fig.
577 1a (IUCN and UNEP-WCMC 2015)). This provides further evidence that vultures in
578 southern Africa, and South Africa in particular, are likely to spend a significant
579 amount of time foraging beyond the boundaries of protected areas, exposing them to
580 multiple threats across the region (Murn and Anderson 2008; Phipps *et al.* 2013a;
581 Phipps *et al.* 2013b).

582 Under future climate conditions the models predicted a decrease in the suitable area
583 covered by protected areas to less than 4% for both models. The largest losses of
584 protected area coverage were predicted in the core breeding range of the Cape
585 vulture in the North West and Limpopo Provinces of South Africa (e.g. the Waterberg
586 Biosphere Reserve), and in northern Namibia (Fig. 1b and c). In contrast, protected
587 areas in the south of the range, such as the Maloti-Drakensberg mountain reserves,

588   were predicted to retain or even gain areas predicted to be suitable under future
589   climatic conditions. Two of the largest remaining Cape vulture colonies are located
590   within protected areas adjacent to or part of the Waterberg Biosphere Reserve
591   (Kransberg in Marakale National Park, and Blouberg in Polokwane Nature Reserve
592   (Mundy *et al.* 1992; BirdLife International 2016)) and were predicted to become
593   unsuitable in the future by both models (Fig. 1 b and c). Although breeding season
594   monitoring indicates that the populations of both colonies are currently stable
595   (Benson 2015; Wolter *et al.* 2016), the predictions from this study that Cape vulture
596   colonies in the north of the range are potentially at greater risk from the effects of
597   climate change than those in the south, and that the Maloti-Drakensberg mountains
598   could play an increasingly important role for breeding vultures in the future, support
599   previous concerns and calls for additional research (Simmons and Jenkins 2007).

600   *4.4. Conservation implications and limitations*

601   The modelling methods used in this study can only provide an approximation of the
602   potential effects of climate change on the distribution of environmentally suitable
603   conditions for Cape vultures and cannot provide definitive information about the
604   underlying mechanisms driving those effects, or predict how vultures will respond to
605   the changing climate in real circumstances (Thuiller *et al.* 2008; Elith and Leathwick
606   2009; Elith *et al.* 2011). Moreover, the future climate data used in this study (a "worst
607   case" scenario) are derived from modelling methods that vary in accuracy regionally,
608   with some variables performing better than others (Braconnot *et al.* 2012; Waltari *et
609   al.* 2014), particularly in southern Africa where high levels of seasonal variance are
610   expected (Winsemius *et al.* 2014). Even so the findings from this study, based on
611   accurate presence locations from tracking data, provide the first evidence to support
612   suggestions that the northern bounds of the Cape vulture range are potentially
613   vulnerable to the effects of future climate change (Simmons and Jenkins 2007).
614   Considering higher temperatures and longer sunlight exposures have been shown to
615   cause higher heat-stress on nesting Cape vultures (Chaudhry 2007) and cliff-nesting
616   seabirds (Oswald and Arnold 2012), and rainfall patterns influence breeding success
617   of other African vulture species (Bridgeford and Bridgeford 2003; Virani *et al.* 2012),
618   it is possible that warming temperatures and changes to precipitation patterns
619   observed over the last few decades (IPCC 2014) may have already affected the
620   breeding distribution of Cape vultures by contributing to the extinction of the

621   Waterberg Plateau breeding colony in north-central Namibia (Simmons and Jenkins

622   2007; Krueger *et al.* 2015). It is unlikely, however, that climate change is solely

623   responsible for the observed declines in Cape vultures in Namibia or elsewhere

624   across their range, and the severe impacts of widespread poisoning (Ogada *et al.*

625   2012; Ogada 2014), fatal interactions with power lines (Boshoff *et al.* 2011), habitat

626   degradation (Bamford *et al.* 2009), food shortages (Krueger *et al.* 2015) and other

627   factors, are widely recognised. Our findings do, however, provide a first indication

628   that climate change might pose an additional serious threat to vultures particularly

629   when considering the potential effects of climate driven changes to vegetation

630   characteristics (Thuiller *et al.* 2006b; Chamaille-Jammes and Fritz 2009) and

631   mammal distributions (Thuiller *et al.* 2006a) that could consequently reduce suitable

632   foraging habitat and carrion availability.

633   It remains unknown exactly how Cape vultures will respond to future climate change

634   in real terms and further related research is required (Simmons and Jenkins 2007;

635   Krueger *et al.* 2015), particularly as this study involves a relatively small sample of

636   individuals. However, if southern areas such as the Maloti-Drakensberg mountains

637   do become more important for Cape vultures in the future, then additional

638   conservation measures to prevent or mitigate the impacts of proposed wind farms

639   (Rushworth and Kruger 2014), power lines (Boshoff *et al.* 2011) and ongoing

640   poisonings (Krueger *et al.* 2015) will be essential throughout their range. In addition,

641   the small proportion of suitable range predicted to occur within protected areas

642   provides further evidence that it will be essential to continue to direct vulture

643   conservation measures to private land as well as to the existing protected area

644   network, as acknowledged for other carnivore species (Lindsey *et al.* 2004; St John

645   *et al.* 2012; Swanepoel *et al.* 2013). From a global perspective, the findings from this

646   study provide a first indication that changing climatic conditions should be

647   considered when planning to mitigate worldwide vulture population declines.

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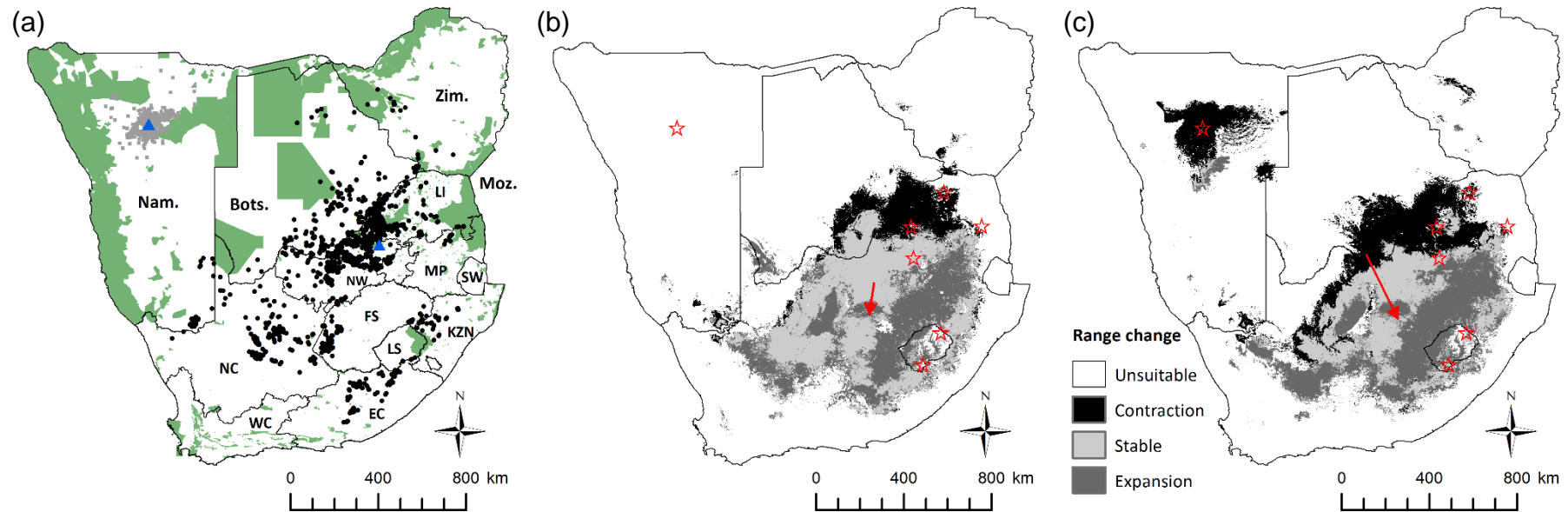652

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Figures and Tables.

Figure 1. (a) Presence locations used for Maxent modelling from GPS tracking data from Cape vultures tagged in South Africa (black circles) and Namibia (dark grey squares). Capture sites are indicated by blue triangles and protected areas are shown by filled green polygons. Letters indicated abbreviated country names and provinces of South Africa (NC = Northern Cape; WC = Western Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumulanga; NW = North West; LI = Limpopo; LS = Lesotho; SW = Swaziland; Nam. = Namibia; Bots. = Botswana; Zim. = Zimbabwe). Areas predicted by Maxent models to be unsuitable in both current and future (2050) climatic conditions (unsuitable), suitable in both (stable), suitable in current but not future conditions (range contraction) and suitable in future but not current conditions (range expansion) are shown by different shaded polygons for (b) Model_SA which was modelled with presence locations from South African tagged vultures only and (c) Model_NamSA which was modelled with all presence locations. The red arrows show to scale the movement of the mean centre of the suitable area under current conditions to the mean centre under future conditions. Red stars indicate some of the main Cape vulture colonies.

Table 1. Mean (±SE), minimum and maximum values for environmental variables in raster cells modelled to be suitable under current and future (2050) climatic conditions using two presence location datasets from Cape vultures fitted with GPS tracking units in South Africa (n=9) and Namibia (n=5). Median and mode values are given for categorical variables. The mean (±SE), minimum and maximum values of the logistic probability of presence for each area of modelled suitability are also provided. The number of grid cells predicted to be suitable by each model are given in parentheses after the model name.

	Model_SA current (n=593,816)			Model_SA 2050 (n=766,707)			Model_NamSA current (n=633,576)			Model_NamSA 2050 (n=650,658)		
Variable*	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
bio_1 (°C)	17.88±0.0029	5.80	22.30	19.98±0.0026	7.50	24.40	18.41±0.0026	6.40	22.20	16.06±0.0022	5.60	21.50
bio_2 (°C)	15.69±0.0013	7.30	19.00	16.10±0.0014	9.90	19.20	15.90±0.0011	11.50	18.90	15.66±0.0013	10.40	18.10
bio_3 (%/10)	5.38±0.0004	4.40	6.40	5.44±0.0003	4.60	6.30	5.48±0.0005	4.40	7.30	5.32±0.0004	4.40	7.30
bio_6 (°C)	1.61±0.0025	-5.90	6.90	3.48±0.0019	-3.00	9.80	2.21±0.0027	-5.90	9.90	0.03±0.0020	-5.90	9.80
bio_12 (mm)	499.49±0.2286	81	1605	495.44±0.2316	77	1218	480.50±0.1938	103	1489	534.90±0.2408	105	1489
bio_15 (%)	72.74±0.0123	35	105	73.88±0.0121	34	98	78.51±0.0187	29	134	66.23±0.0130	20	136
bio_19 (mm)	21.58±0.0199	2	326	24.09±0.0172	3	333	17.47±0.0163	0	235	29.12±0.0157	0	233
Alt (m asl)	1222.61±0.3567	517	3084	1346.14±0.3225	596	3308	1248.70±0.3199	519	2946	1420.00±0.3349	389	3143
ndvi_aug (NDVI*1000)	103.91±0.0189	10	245	100.67±0.0169	10	255	101.56±0.0157	10	185	101.06±0.0165	10	223
slope_perc (%)	2.23±0.0049	0	52.01	2.38±0.0042	0	52.01	1.75±0.0039	0	52.55	2.59±0.0047	0	52.55
FAOcattle05 (cattle·km^{-1})	10.53±0.0152	0	121.94	11.74±0.0165	0	468.60	9.34±0.0141	0	468.60	13.31±0.0234	0	468.60
Probability of presence	0.48±0.0001	0.31	0.89	0.55±0.0002	0.31	0.93	0.46±0.0001	0.31	0.88	0.59±0.0002	0.31	0.97
Categorical variables	Median (Mode)			Median (Mode)			Median (Mode)			Median (Mode)		
rum_prod_system	2 (2)			4 (2)			2 (2)			4 (2)		
GLC2000	14 (14)			14 (14)			14 (14)			14 (14)		
WWF_ecoregion_ID	31009 (31309)			31009 (31009)			31009 (31309)			31009 (31009)		

*bio_1 = annual mean temperature; bio_2 = mean diurnal temperature range; bio_3 = isothermality (%/10); bio_6 = minimum temperature of the coldest week; bio_12 = annual precipitation; bio_15 = precipitation seasonality (% - coefficient of variation); bio_19 = precipitation of the coldest quarter; Alt = elevation above sea level; ndvi_aug = NDVI in August (NDVI*1000); slope_perc = slope percent rise; FAOcattle05 = FAO cattle density; rum_prod_sys = FAO ruminant production systems (2 = Livestock-only systems in arid areas; 4 = Livestock-only systems in temperate areas or tropical highlands); GLC2000 = Global Land Cover from the year 2000 (14 = Open grassland with sparse shrubs); WWF_ecoregion_ID = WWF ecoregion (31009 = Highveld grasslands; 31309 = Kalahari xeric savannah). Refer to 'Environmental Data' in Supporting Information.

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