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

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Abstract

Multiple anthropogenic threats have caused vulture populations to decline globally, with serious ecological and socio-economic implications. The Cape vulture (*Gyps coprotheres*) has declined throughout its range in southern Africa, recently being listed as extinct as a breeding species in Namibia. It has been suggested that climate change might have contributed to the decline of Cape vultures in northern parts of the range. To provide a first assessment of the potential impacts of climate change on the occurrence of Cape vultures, a presence-only ecological niche modelling method (Maxent) was used to predict the spatial occurrence patterns of wild-caught vultures fitted with GPS tracking units in northern Namibia and northern South Africa, under current and future climatic conditions. The models showed high predictive power (AUC >0.868±0.006), with precipitation seasonality and other bioclimatic variables identified as the most important variables for predicting Cape vulture presence. Of the area estimated to be suitable for Cape vultures under current conditions, 28-55% was predicted to become unsuitable under future climate conditions, with a pole-ward shift in the mean centre of the range of 151-333 km and significant range loss from the former breeding range in north-central Namibia and the core breeding range in northern South Africa. Expansions of suitable conditions into areas where the species has been historically absent in the south of the range were also predicted. The coverage of predicted suitable areas by protected areas was predicted to decrease from 5.8-7.9% to 2.8-3.8%, suggesting that private land will become increasingly important for Cape vulture conservation.

Keywords:

Gyps vulture; climate change; environmental niche modelling; protected area; range shift; telemetry.

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 the development and spread of disease (Sekercioglu 2006; Moleon *et al.* 2014; Morales-Reyes *et al.* 2015)). However, despite an increasing number of remote tracking studies on African vulture species (Phipps *et al.* 2013a; Spiegel *et al.* 2013; Kendall *et al.* 2014; Krueger *et al.* 2014) to our knowledge there has been no attempt to investigate what drives their spatial distribution using GPS tracking data and multivariate ENM methods.

The Cape vulture (*Gyps coprotheres*) is endemic to southern Africa and is listed as Endangered on the IUCN Red List due to recently estimated population declines of -92% over three generations (48 years), at a median annual rate of -5.1% (Ogada *et al.* 2015b; BirdLife International 2016). It is a gregarious cliff-nesting species with a global population estimated at 8,000–10,000 individuals (circa 4,000 breeding pairs) (BirdLife International 2016). The largest remaining breeding colonies are located in the north-eastern provinces of South Africa with smaller, more dispersed colonies in the Maloti-Drakensberg mountains of Lesotho and south-east South Africa (Rushworth and Kruger 2014; Wolter *et al.* 2016). An isolated breeding colony located on the cliffs of the Waterberg Plateau Park in north-central Namibia that numbered 500 Cape vultures in 1940 was reduced to as few as 13 individuals in 1985 (Brown 1985) and the species has recently been classified as extinct as a breeding species in the country (BirdLife International 2016). The declines have been mainly attributed to the widespread use of poisons for killing predators in the region and the loss of foraging habitat due to shrub encroachment (Brown 1985; Mundy *et al.* 1992; Bamford *et al.* 2007; Schumann *et al.* 2008; Bamford *et al.* 2009).

It has also been suggested that climate change may have played a role in the extinction of Cape vulture colonies in the north of their range since the 1950s due to the increasing temperatures and changing rainfall patterns recorded in the region during that time period (Simmons and Jenkins 2007; IPCC 2014). Southern Africa, and Namibia in particular, is predicted to experience particularly significant changes to climatic conditions (e.g. rising temperatures and altered rainfall patterns (Conway *et al.* 2015; van Wilgen *et al.* 2016)) which are expected to drive pole-wards range shifts and loss of climatically suitable conditions for many species from different taxa (Simmons *et al.* 2004; Thuiller *et al.* 2006b; Midgley and Thuiller 2011; Garcia *et al.* 2012). There is evidence to suggest that breeding Cape vultures suffer increased levels of heat stress in higher temperatures and longer sunlight exposures

(Chaudhry 2007); rainfall patterns influence vulture breeding success (Bridgeford and Bridgeford 2003; Virani *et al.* 2012); and increased temperatures and carbon dioxide levels enhance woody vegetation cover (Midgley and Bond 2015), inhibiting the visual foraging of vultures by obscuring carcasses (Bamford *et al.* 2009). Simmons and Jenkins (2007) therefore propose that climate change may work in concert with other factors to push Cape vultures away from their northernmost colonies in a southwards direction, and further work is required to investigate the potential impacts of climate change on Cape vulture occurrence (Krueger *et al.* 2015).

In this study we use Maxent modelling to provide a first description of the spatial niche characteristics for Cape vultures and identify some of the environmental factors driving their occurrence. The presence locations were derived from GPS tracking data from wild caught vultures from northern South Africa (Phipps *et al.* 2013b) and from some of the last remaining Cape vultures in Namibia (Bamford *et al.* 2007). We investigate the potential influence of climate change on the extent of areas predicted to be currently suitable by projecting the models onto future bioclimatic conditions. We compare results from models using only data from South African tagged vultures with models from data from all vultures to assess whether conditions in north-central Namibia are predicted to be suitable for Cape vultures under current and future climate scenarios. We also evaluate the coverage provided by protected areas to areas modelled to be suitable for Cape vultures under current and future conditions as species turnover in protected areas is expected to be high in the region (Hole *et al.* 2009). The intention of this study is to provide a first description of the spatial niche of a sample of Cape vultures from the core breeding range of the species and to assess whether vulture occurrence patterns might be influenced by global climate change.

2. Methods

2.1. Modelling method and study area

The presence-only method Maxent (Phillips *et al.* 2006) was used to model the ecological niche of the Cape vulture as it does not require true absence data (Elith *et al.* 2011) and has been used previously with avian tracking data obtained from a small number of individuals (Gschweng *et al.* 2012; Liminana *et al.* 2012; Liminana *et al.* 2014). The geographical area used for ecological niche modelling was delineated by the national borders of South Africa, Lesotho, Swaziland, Zimbabwe, Botswana and Namibia, to correspond with the historical distribution of the Cape vulture (Mundy *et al.* 1992; BirdLife International 2016).

2.2. GPS tracking and presence data

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

Two datasets of presence locations were selected for modelling purposes. Firstly, one dataset consisted of GPS locations only obtained from the nine South African tagged vultures, while the second consisted of GPS locations from all 14 vultures. This was done to compare results based on data from only South African tagged birds (i.e. captured in the “core” of the species’ breeding range (Mundy *et al.* 1992; BirdLife International 2016)) to those that included presence locations from Namibia where the species formerly bred but is now considered extinct as a breeding species (Brown 1985; BirdLife International 2016). This provided an indication of the suitability of environmental conditions in northern Namibia compared to the rest of the study area and whether or not the region was predicted to be more or less affected by climate change compared to more southern areas during subsequent analyses.

Spatial preparation of GPS location and environmental variable data was performed in SDMtoolbox v1.1b (Brown 2014) in ArcMap (ESRI 2014) with all data projected to the Africa Albers Equal Area Conic coordinate system. For both presence datasets only stationary (<10 kmh^{-1}) GPS locations were selected to more accurately represent actual use of a given area. The Namibian tracking dataset was filtered further by only including GPS locations recorded every two hours from 09:00 to 17:00 CAT to reduce spatial autocorrelation and to correspond with the diurnal activity patterns of the vultures (Bamford *et al.* 2007). To further reduce spatial autocorrelation, which can influence species distribution model performance (Boria *et al.* 2014), the presence locations for each individual vulture were filtered by using the *spatially rarefy occurrence data* tool in SDMtoolbox v1.1b (Brown 2014) in ArcMap (ESRI 2014) to reduce clusters of presence locations to a single presence location within a Euclidean distance of 1 km. In order to reduce the influence of the disparity in tracking periods, and therefore the number of GPS locations per individual (Gschweng *et al.* 2012; Liminana *et al.* 2014), the mean number of stationary GPS locations rarefied by 1 km for the nine South African tagged vultures was calculated (mean±SD = 238±151 GPS locations per individual) and used to select a random subsample of 238 GPS locations for all individuals for which more than 238 stationary rarefied GPS locations were available using statistical software R v3.1.1 (R Core Team 2014). The maximum number of GPS locations per vulture was therefore limited to 238 and all stationary rarefied GPS locations were retained for vultures with less than 238 stationary rarefied GPS locations. Finally, the GPS locations for all individuals were merged into one shapefile and further spatially rarefied to a Euclidean distance of 1km. The two final presence location datasets consisted of 1437 presence locations for the South African tagged individuals and 2123 presence locations for the South African and Namibian tagged vultures combined (i.e. 686 presence locations for the five Namibian vultures; Fig. 1a).

Capture and tagging procedures were approved by the ethical review committee of the School of Animal, Rural and Environmental Science, Nottingham Trent University, and permits were granted by the Department of Agriculture, Conservation, Environment and Rural Development, North West Provincial Government, Republic of South Africa (Permit: 000085 NW-09) and the Namibian Ministry of Environment and Tourism (Permit: 1578/2004-2005). All procedures were carried out by South African Bird Ringing Unit permit holders.

2.3. Environmental variables

Only environmental variables with a pairwise Pearson's correlation coefficient of less than 0.7 (assessed using SDMtoolbox v1.1b (Brown 2014)) were included in the modelling process to reduce multi-collinearity effects (Phillips and Dudik 2008). Environmental variables were subsequently selected based on prior knowledge of their ecological relevance to Cape vultures and their contribution to preliminary models in an effort to achieve parsimony to reduce the risk of over-fitting (Anderson and Gonzalez 2011; Van Gils *et al.* 2014). The models included a total of 14 environmental variables (Table 1, Table A1) at a spatial resolution of 30 arc-seconds (approximately 1 km^2 at the equator): seven bioclimatic variables from the WorldClim database (http://www.worldclim.org/; (Hijmans et al. 2005)); two topographic variables (elevation and slope) derived from the digital elevation model (DEM) data from the WorldClim database; Normalised Difference Vegetation Index (NDVI) data for August derived from the SPOT (Satellite Pour l'Observation de la Terre; http://www.cnes.fr/web/CNES-en/1415-spot.php) program; the Food and Agriculture Organisation (FAO) global cattle density dataset (FAOcattle05; http://www.fao.org; (Robinson et al. 2007)); the FAO ruminant production systems dataset (Robinson et al. 2011)); Global Land Cover 2000 (Mayaux et al. 2004); and the World Wildlife Fund (WWF) terrestrial ecoregions of the world dataset classified by ecoregion ID code (http://www.worldwildlife.org/biome-categories/terrestrial-ecoregions; (Olson et al. 2001)). Similar variables have previously performed well when modelling bird distributions (Barbet-Massin *et al.* 2009; Jiguet *et al.* 2011; Liminana *et al.* 2012; Liminana *et al.* 2014) and are known to influence vulture flight patterns (e.g. isothermality; (Pennycuick 1972; Harel *et al.* 2016)) and the availability of carrion due to seasonal changes in ungulate mortality driven by fluctuations in vegetation productivity (Houston 1974b; Mduma *et al.* 1999; Owen-Smith *et al.* 2005; Ogutu *et al.* 2008). More detailed information on the selection of environment variables can be found in the "Environmental Data" section in Supporting Information.

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

2.4. Ecological niche modelling procedure

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

Variable importance was assessed using two heuristic tests (percent contribution and permutation importance) and the jacknife procedure in Maxent. Percent contribution was calculated as the proportional contribution of each variable to the model training gain which is dependent on the path of the Maxent algorithm (Phillips *et al.* 2006). The permutation importance metric is independent of the algorithm path and represents the influence of the given variable on the training AUC value, normalized to percentages (Phillips *et al.* 2006). For the jacknife tests variables were successively omitted and then used in isolation to measure their relative and absolute contribution to model gain, providing a measure of their explanatory power when considered alone (Elith *et al.* 2011; Gschweng *et al.* 2012).

2.5. Assessment of environmental suitability and impact of climate change

The logistic output from the Maxent model was used to display the spatial predictions of the probability of Cape vulture presence across the study area with values ranging from 0 to 1 (Phillips and Dudik 2008). To classify the model predictions into areas of binary suitability (1) and unsuitability (0) the mean (0.31) of the maximum training sensitivity plus specificity logistic threshold (*MaxTSS*) for the model with only South African tagged vulture presences (*MaxTSS* = 0.28) and the model with both presence datasets (*MaxTSS* = 0.33) was used. The *MaxTSS* threshold is independent of prevalence of presence locations and is recommended for use with presence only data as an objective method of binary suitability threshold selection (Jiguet *et al.* 2011; Liu *et al.* 2013). Binary maps of suitability were created using this method for both current and future (for the year 2050) climatic conditions for the two different presence datasets on which the models were based (i.e. *Model_SA =* presence locations from South African tagged vultures; *Model_NamSA* = presence locations from both South African and Namibian tagged vultures). Subsequently the areas predicted to be unsuitable and suitable were compared for each model separately under the current and future environmental conditions. This was done in ArcMap to produce a raster dataset with areas predicted to be unsuitable in both current and future conditions; suitable under current but not future environmental conditions (range contraction); unsuitable under current conditions but suitable under future conditions (range expansion); and suitable under both current and future conditions (stable range). The distance between the mean centres of the extent of the suitable areas under current and future conditions was calculated in ArcMap to quantify the directional range shift from current to future conditions.

2.6. Evaluation of protected area coverage

To assess the level of protection afforded to areas predicted as suitable for Cape vultures based on the binary suitability maps, the number of suitable raster cells located within nationally and internationally designated protected areas in the 2015 World Database on Protected Areas (IUCN and UNEP-WCMC 2015) were counted for current and future models in ArcMap (Liminana *et al.* 2012; Swanepoel *et al.* 2013; Liminana *et al.* 2014).

3. Results

3.1. Ecological niche model description and variable importance

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

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

According to the heuristic tests of variable importance bioclimatic variables were the most influential to model predictions in terms of percent contribution and permutation importance (Fig. A2), with precipitation seasonality (*Bio_15*) contributing 29.88±2.14% (35.98±2.72% permutation importance) to Model_SA and five bioclimatic variables (*Bio_2, 12, 6, 3 and 1* in descending order) collectively contributing 73.70% to Model_NamSA (Fig. A2). The four variables that contributed the most to Model_SA (*Bio_15, 6, 12 and 19* in descending order) collectively contributed 70.44% to the model. Elevation (*alt*) was also a relatively important variable with a permutation importance of 20.99% for Model_NamSA and 10.08% for Model_SA. The jacknife tests for variable importance identified precipitation seasonality (*Bio_15*) as the most important variable for both models, followed by precipitation of the coldest quarter (*Bio_19*), minimum temperature of the coldest week (*Bio_6*) and WWF ecoregion ID for Model_SA (Fig. A2). WWF ecoregion ID was also identified as an important variable for Model_NamSA, followed by altitude, minimum temperature of the coldest week (*Bio_6*) and NDVI in August (Fig. A2). According to the jacknife tests exclusion of the variables from the models did not identify any obvious single variable that contained information that was lacking in the other variables, although the omission of precipitation seasonality (*Bio_15*) and isothermality (*Bio_3*) resulted in the greatest decrease in gain for Model_SA and Model_NamSA, respectively (Fig. A2).

The average variable values for raster cells predicted to be suitable for Cape vultures were similar for Model_SA and Model_NamSA (Table 1). The elevational range of cells predicted to be suitable for Cape vulture occurrence under current conditions for both models was 517 – 3 308 m·asl compared to 389 – 3 148 m·asl under future conditions. For all models, cells predicted to be suitable for Cape vulture occurrence tended to consist, on average (median and mode), of “livestock-only ruminant production systems in arid areas” with mean (±SE) cattle densities from 9.34±0.014 cattle·km^{-1} (Model_NamSA current) to 13.31±0.023 cattle·km^{-1} (Model_NamSA 2050), in areas of “open grassland with sparse shrubs” land-cover in the Highveld grasslands or Kalahari xeric savannah ecoregions (Table 1).

3.2. Projected extent of predicted environmental suitability

Of the 460,801 km^2 predicted by Model_SA to be suitable for Cape vultures under current conditions, 28% was predicted to become unsuitable in 2050 with a pole-ward 151 km shift of the mean centre of the suitable area (Fig. 1b). However, under future conditions the overall suitable area was predicted to increase from 15% to 19% (594,964 km^2) of the study area, of which 44% (264,070 km^2) extended into areas predicted to be unsuitable in current conditions (Fig. 1b). For Model_NamSA a greater degree of current suitable range loss was predicted, with 55% of the 491,655 km^2 current suitable range predicted to become unsuitable in 2050, with a pole-ward 333 km shift of the mean centre of the suitable area (Fig. 1c). 56% (284,662 km^2) of the area predicted to be suitable in 2050 was predicted to be unsuitable in current conditions, resulting in a relatively small increase in the area predicted to be suitable across the study area to 504,911 km^2 (Fig. 1c). Both models predicted that the largest area of range contraction would be in the western half of the Limpopo Province, South Africa, and south-east Botswana (Fig. 1b and c). Almost the whole area in north-central Namibia predicted to be suitable under current conditions by Model_NamSA was predicted to become unsuitable under climatic conditions in 2050 (Fig. 1c; Fig. A1). The mean elevation (*alt*) for areas predicted to be suitable increased by 124 m and 171 m for Model_SA and Model_NamSA, respectively (Table 1).

3.3 Protected area coverage under current and projected suitability

Of the area predicted by Model_SA to be suitable for Cape vultures, 5.85% (26 961 km^2) and 3.79% (22 560 km^2) was included within protected areas under current and future conditions, respectively. The protected areas covering more than 1,000 km^2 of suitable area under current conditions were the Waterberg Biosphere Reserve (BR) in Limpopo Province, South Africa, the Drakensberg World Heritage Site (WHS), and the Central Kalahari Game Reserve (GR) in south-east Botswana, whereas under future conditions only the Kalahari-Gemsbok National Park (NP) and the Drakensberg WHS covered more than 1,000 km^2. For Model_NamSA, 7.91% (38,874 km^2) and 2.77% (13,963 km^2) of the predicted suitable area was included within protected areas under current and future conditions, respectively. The protected areas covering more than 1,000 km^2 of suitable area under current conditions were several conservancies in north-central Namibia, the Waterberg BR in Limpopo Province, South Africa, and the Central Kalahari GR in south-east

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

4. Discussion

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

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

of suitable area for the model based only on data from South African tagged vultures) was small and predicted to decrease under future conditions.

4.1. Influence of environmental variables on predicted probability of presence

Overall, bioclimatic variables, and precipitation seasonality in particular, were the most influential in both models, which is consistent with previous studies that used GPS tracking data to model the ecological niche of raptors (Gschweng *et al.* 2012; Liminana *et al.* 2012). Vegetation production is dependent on climatic conditions and precipitation patterns determine forage abundance and quality, and subsequently nutrition-related mortality rates for ungulates (Boone *et al.* 2006; Ogutu *et al.* 2008; Chamaille-Jammes and Fritz 2009). Vulture movement patterns have been shown to be closely associated with seasonal ungulate mortality rates driven by seasonal changes in vegetation productivity indicated by changes in NDVI, with tracked vultures preferring to forage in areas with higher ungulate mortality during the dry season in the Masai Mara, Kenya (Kendall *et al.* 2014). NDVI in August was identified as the most important variable in the preliminary model which included only the twelve monthly NDVI variables, as well as for both models including all variables. As August is one of the coldest and driest months in southern Africa and mortality of both wild and domestic ungulates can be relatively high during that time as a consequence of nutritional stress (Owen-Smith *et al.* 2005; Mapiye *et al.* 2009), it is likely that the models reflect the influence of seasonal vegetation production on Cape vulture occurrence by affecting the availability of carrion. Correspondingly, the probability of Cape vulture presence was highest in areas with very low levels of precipitation during the coldest quarter (*Bio_19*; Fig. A3b) and temperatures of 2^{o}C to 5^{o}C in the coldest week (*Bio_6*; Fig. A3c), which would result in seasonal periods of low grass productivity and potentially higher ungulate mortality rates (Owen-Smith 2008). These results suggest that bioclimatic factors might play a role in driving Cape vulture occurrence and movement patterns, most likely through climatic effects on vegetation production which directly influences the availability of food in the form of ungulate carrion, as reported for vultures in Kenya (Kendall *et al.* 2014). This provides a partial explanation (together with the availability of cliff nesting sites) for why the core breeding and foraging ranges of the species are located in the northern provinces of South Africa which are characterised by distinct wet summer (October – April) and dry winter (May – September) seasons (Benson *et al.* 1990; Mundy *et al.*

1992; Borello and Borello 2002), as Cape vultures and other *Gyps* species tend to coincide their breeding seasons with the highest availability of ungulate carrion in the dry season (Houston 1974b; Piper *et al.* 1999; Virani *et al.* 2010; Virani *et al.* 2012). This is consistent with previous studies that have found an inverse relationship between vulture breeding success and rainfall in the previous year due to reduced ungulate carrion availability (Bridgeford and Bridgeford 2003; Virani *et al.* 2012).

As large soaring fliers, vultures are reliant on suitable climatic conditions to provide sufficient air currents and thermals to allow them to cover the large distances required to locate their naturally ephemeral food source and it has been suggested that high rainfall and adverse weather conditions limit their ability to do so (Pennycuick 1972; Lambertucci and Ruggiero 2013; Harel *et al.* 2016). The influence of local climatic factors such as temperature range and precipitation in determining the occurrence of large soaring birds has been shown for the Andean condor (*Vultur gryphus*), which should, according to a modelling study, prefer roost sites on climatically stable cliffs in areas of low rainfall (Lambertucci and Ruggiero 2013). The importance of isothermality (a measure of diurnal and annual temperature ranges) in both models (*Bio_3*; Fig. A3f) and the higher probabilities of occurrence in areas with moderate seasonal rainfall, are consistent with this and possibly reflect the influence of meteorological variables on the local flying conditions for large vultures which tend to require strong up-draughts and drier conditions (Shepard and Lambertucci 2013; Harel *et al.* 2016).

African vultures locate carcasses by sight alone (Houston 1974a) and it has been shown that high tree densities reduce their ability to locate and land at carcasses, decreasing their foraging efficiency (Schultz 2007; Bamford *et al.* 2009). The results from this study provide further evidence that vegetation and habitat characteristics influence vulture movement and occurrence patterns. WWF ecoregion ID was identified as an important variable for both models, with higher probabilities of Cape vulture presence in habitats characterised by relatively limited tree density and more open habitats (e.g. highveld grassland and southern African bushveld (Olson *et al.* 2001)). In addition, the most prevalent land cover type in the modelled suitable areas was open grassland with sparse shrubs which is also defined by relatively low tree densities (Table 1 (Mayaux *et al.* 2004)). These results correspond with previous descriptions of suitable Cape vulture habitat (Mundy *et al.* 1992) and support suggestions that they avoid heavily wooded areas and might be susceptible to the increasing rate and extent of bush encroachment in southern Africa (Schultz 2007; Bamford *et al.* 2009).

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

4.2. Projected influence of climate change

The pole-ward shifts and increase in mean altitude of areas predicted to be suitable for Cape vultures in 2050 by both models correspond with previous studies that have predicted similar responses to changing climatic conditions in bird species in southern Africa (Simmons *et al.* 2004; Hole *et al.* 2009; Willis *et al.* 2009; BirdLife International and Durham University 2015). Although the model that used presence locations from Namibian tagged vultures predicted an area of suitability in the north-central region of the country (Fig. 1c and A1c), the model that only used presence locations from South African tagged vultures predicted a very low probability of presence in the same area (Fig. 1b and A1a). This indicates that bioclimatic conditions are very different in north-central Namibia compared to the majority of the predicted suitable area in South Africa and south-east Botswana (Williams *et al.* 2007). Under future conditions the area modelled to be suitable in north-central Namibia was predicted to contract away from its current extent in a southwards direction more than 170 km from the former Cape vulture breeding colony on the cliffs of the Waterberg Plateau (Fig. 1c). This is consistent with previous studies that predict that northern Namibia is likely to be particularly vulnerable to the effects of climate change as current climatic conditions shift pole-wards or even disappear, causing high rates of range loss for a high number of species from different taxa (Thuiller *et al.* 2006a; Thuiller *et al.* 2006b; Williams *et al.* 2007; Garcia *et al.* 2012). Significant range loss was also predicted by both models in the current core breeding range of Cape vultures in northern South Africa and south-east Botswana (Fig. 1b and c), areas which have previously been predicted to undergo high levels of bird and mammal species turnover and range loss driven by climate change (Thuiller *et al.* 2006a; Hole *et al.* 2009). These modelled patterns of range contraction support the suggestion that the most northernmost Cape vulture breeding colonies could be at risk of becoming climatically unsuitable for the species in the future, and that climate change might have already played a role in the extinction of the only breeding colony in northern Namibia (Simmons and Jenkins 2007). Correspondingly, recent colony surveys indicate that while several peripheral, northern colonies have been abandoned, the core breeding population in the Magaliesberg mountains remains stable, where an increase in supplementary carrion at vulture feeding sites might have led to higher local survival rates and recruitment from more peripheral colonies (Wolter *et al.* 2016), potentially mitigating any adverse impacts of climate change. The influence and interaction of these factors requires further investigation, however.

In contrast to the loss of suitable areas in the north of the modelled range, an increase in the overall extent of the suitable area was predicted by both models, largely as a result of a southwards range expansion into the highveld grassland of the Free State and south-west Mpumalanga Provinces (Fig. 1b and c). This region is considered to be outside the historical distribution of the Cape vulture partly due to the relatively long distances from major breeding colonies but also due to the relatively low abundance of trees for roosting and perching after long-term overgrazing suppression and habitat degradation (Mundy *et al.* 1992; Low and Rebelo 1998; Olson *et al.* 2001). Therefore, although large bodied species, such as Cape vultures, that exhibit evidence of nomadic-like movements (Phipps *et al.* 2013a; Phipps *et al.* 2013b) are predicted to be more capable of dispersing to suitable areas under future climate change scenarios (Simmons *et al.* 2004; Dodge *et al.* 2014), dispersal capabilities were not considered in this study and so any predicted range expansions should be considered with caution, particularly as there are no active breeding colonies in the area and other factors such as land use change were not accounted for (Guisan and Thuiller 2005). Nevertheless, fluctuating carrion availability regularly forces vultures to shift their movement patterns (Kendall *et al.* 2014), and they even forage beyond their historical distribution by perching on newly constructed power line structures in areas previously devoid of natural perches (Phipps *et al.* 2013b), indicating that they might show a degree of plasticity in their movement patterns in response to future climate change (Simmons *et al.* 2004; Dodge *et al.* 2014).

4.3. The current and future role of protected areas

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

Under future climate conditions the models predicted a decrease in the suitable area covered by protected areas to less than 4% for both models. The largest losses of protected area coverage were predicted in the core breeding range of the Cape vulture in the North West and Limpopo Provinces of South Africa (e.g. the Waterberg Biosphere Reserve), and in northern Namibia (Fig. 1b and c). In contrast, protected areas in the south of the range, such as the Maloti-Drakensberg mountain reserves, were predicted to retain or even gain areas predicted to be suitable under future climatic conditions. Two of the largest remaining Cape vulture colonies are located within protected areas adjacent to or part of the Waterberg Biosphere Reserve (Kransberg in Marakale National Park, and Blouberg in Polokwane Nature Reserve (Mundy *et al.* 1992; BirdLife International 2016)) and were predicted to become unsuitable in the future by both models (Fig. 1 b and c). Although breeding season monitoring indicates that the populations of both colonies are currently stable (Benson 2015; Wolter *et al.* 2016), the predictions from this study that Cape vulture colonies in the north of the range are potentially at greater risk from the effects of climate change than those in the south, and that the Maloti-Drakensberg mountains could play an increasingly important role for breeding vultures in the future, support previous concerns and calls for additional research (Simmons and Jenkins 2007).

4.4. Conservation implications and limitations

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

Waterberg Plateau breeding colony in north-central Namibia (Simmons and Jenkins 2007; Krueger *et al.* 2015). It is unlikely, however, that climate change is solely responsible for the observed declines in Cape vultures in Namibia or elsewhere across their range, and the severe impacts of widespread poisoning (Ogada *et al.* 2012; Ogada 2014), fatal interactions with power lines (Boshoff *et al.* 2011), habitat degradation (Bamford *et al.* 2009), food shortages (Krueger *et al.* 2015) and other factors, are widely recognised. Our findings do, however, provide a first indication that climate change might pose an additional serious threat to vultures particularly when considering the potential effects of climate driven changes to vegetation characteristics (Thuiller *et al.* 2006b; Chamaille-Jammes and Fritz 2009) and mammal distributions (Thuiller *et al.* 2006a) that could consequently reduce suitable foraging habitat and carrion availability.

It remains unknown exactly how Cape vultures will respond to future climate change in real terms and further related research is required (Simmons and Jenkins 2007; Krueger *et al.* 2015), particularly as this study involves a relatively small sample of individuals. However, if southern areas such as the Maloti-Drakensberg mountains do become more important for Cape vultures in the future, then additional conservation measures to prevent or mitigate the impacts of proposed wind farms (Rushworth and Kruger 2014), power lines (Boshoff *et al.* 2011) and ongoing poisonings (Krueger *et al.* 2015) will be essential throughout their range. In addition, the small proportion of suitable range predicted to occur within protected areas provides further evidence that it will be essential to continue to direct vulture conservation measures to private land as well as to the existing protected area network, as acknowledged for other carnivore species (Lindsey *et al.* 2004; St John *et al.* 2012; Swanepoel *et al.* 2013). From a global perspective, the findings from this study provide a first indication that changing climatic conditions should be considered when planning to mitigate worldwide vulture population declines.

Figures and Tables.

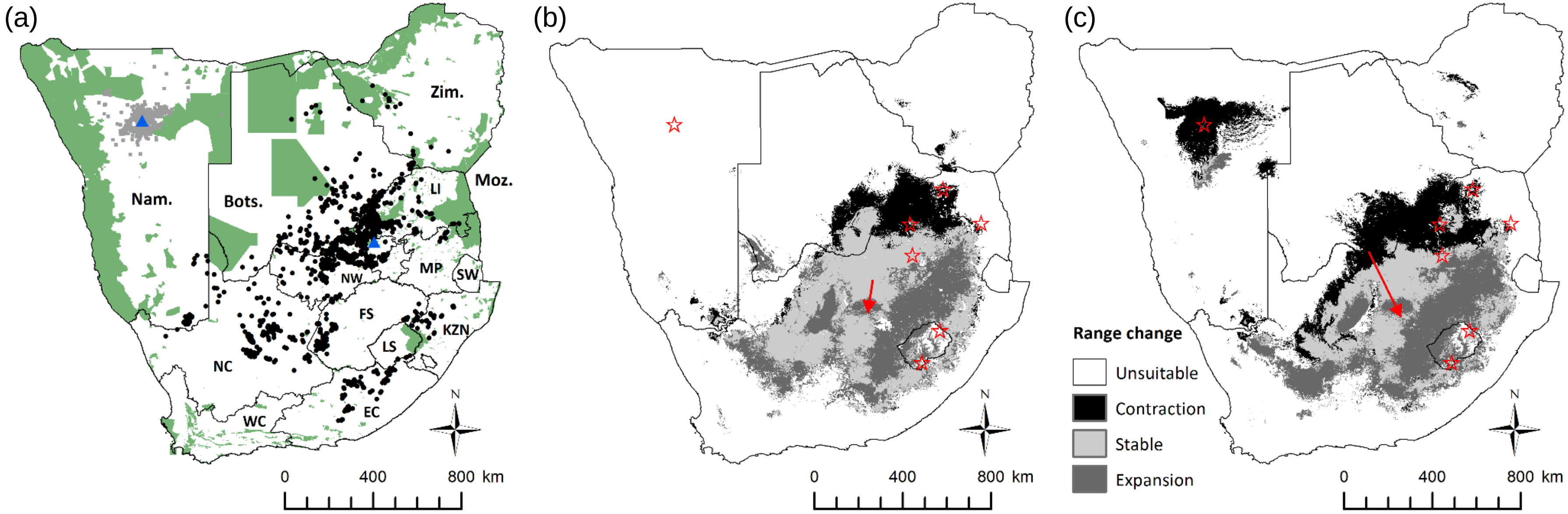

Figure 1. (a) Presence locations used for Maxent modelling from GPS tracking data from Cape vultures tagged in South Africa (black circles) and Namibia (dark grey squares). Capture sites are indicated by blue triangles and protected areas are shown by filled green polygons. Letters indicated abbreviated 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 (ºC)	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 (ºC)	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 (ºC)	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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