

**Predicting the impacts of climate change on Papio baboon biogeography:  
Are widespread, generalist primates 'safe'?**

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# **Predicting the impacts of climate change on *Papio* baboon biogeography: are widespread, generalist primates ‘safe’?**

Running title: Impacts of climate change on baboons

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## Acknowledgements

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## ABSTRACT

**Aims:** To explore whether wide-ranging, generalist primates like baboons can be presumed ‘resilient’ in the face of climate change. We identify the main environmental variables influencing the baboon species’ current distributions; map their current potential distributions; and predict and evaluate their future potential distributions under different climate change scenarios.

**Location:** Africa and Arabia.

**Taxon:** Baboons, *Papio* spp.

**Methods:** We used presence localities for olive, yellow, Guinea, hamadryas, chacma and kinda baboons together with high-resolution data on 19 bioclimatic variables, altitude and vegetation to construct species distribution models (SDMs) for each taxon. These SDMs were run under current and future conditions, with future models based on three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.5 and 6.0) for 2050 and 2070 to explore a range of different possible futures.

**Results:** All SDMs produced AUC values >0.94 suggesting excellent overall performance. Altitude was the most important variable influencing Guinea baboon distributions (contributing 39.6%), annual precipitation for the olive (34.1%), precipitation of the driest month for the hamadryas (21.1%) and precipitation of the warmest quarter for the yellow, kinda and chacma baboons (41.4%, 40.2% and 21.7% respectively). The Guinea, chacma and kinda baboons are all predicted to suffer substantial habitat loss by 2070 under RCP6.0. In contrast, all models for the olive and hamadryas baboons predicted an increase in suitable habitat and no substantial changes were predicted for the yellow baboon.

**Main conclusions:** Three of six baboons are at significant risk of range loss as climates warm despite their apparent behavioural and ecological flexibility. The Guinea baboon, IUCN listed as Near Threatened, and the chacma baboon (Least Concern) will probably be worst affected, followed by the kinda. We recommend more focus on biogeographic tools as a means of exploring potential vulnerabilities in seemingly resilient (primate and non-primate) species.

**KEYWORDS:** Africa, baboons, biogeography, climate change, generalist, MaxEnt, *Papio*, species distribution modelling

## INTRODUCTION

Anthropogenic climate change, alongside habitat destruction, is driving a global biodiversity crisis by hastening extinctions, changing species' distributions and restructuring ecosystems (Bellard, Bertelsmeier, Leadley, Thuiller & Courchamp, 2012). The effects have been explored in a wide array of species (e.g. plants: Thuiller, Lavorel, Araújo, Sykes & Prentice, 2005; animals: Bale et al., 2002; Rijnsdorp, Peck, Engelhard, Möllmann & Pinnegar, 2009; Crick, 2004). Some seem more susceptible than others. Resilient species are able to shift their ranges or adapt rapidly enough to out-run ongoing changes; those that cannot are at greater risk of extinction (Hill, Griffiths & Thomas, 2011). Overall, tropical species seem to be more threatened than those in subtropical and temperate regions (Khaliq, Hof, Prinzing, Böhning-Gaese & Pfenninger, 2014) and Africa, in particular, is thought to be the worst affected continent (Leal Filho, Esilaba, Rao & Sridhar, 2016; Lovett, Midgley & Barnard, 2005). This is bad news for Africa's 111 non-human primates, facing risks from climate change, logging, mining, the expansion of agriculture, hunting and other anthropogenic stressors (Estrada et al., 2017).

Recent assessments of primate extinction risks, however, found that 37% of mainland African species were threatened (compared to 55% globally) and 42% are in decline (versus 75% overall; Estrada et al., 2017). Some of the difference may result from the presence in Africa of some remarkably flexible, ecologically generalist species like the *Papio* baboons, which adapt effectively to many anthropogenic contexts (Bergman & Kitchen, 2008; Hoffman & O'Riain, 2012; Warren, 2008; Winder, 2015). The genus *Papio* comprises six closely-related taxa (Zinner, Wertheimer, Liedigk, Groeneveld & Roos, 2013), usually given specific status even though several hybridise in contact zones (Jolly, Burrell, Phillips-Conroy, Bergey & Rogers, 2011). They are thought to have begun diverging approximately 2.09 million years ago (Zinner, Groeneveld, Keller & Roos, 2009), and collectively occupy most of sub-Saharan Africa (Winder, 2015). The IUCN Red List classifies the Guinea baboon, which has the smallest range, as Near Threatened and the others as species of Least Concern (IUCN, 2017).

It would be easy to assume that the wide ranges, large populations and ecological flexibility of the *Papio* baboons will make them less susceptible to negative impacts of climate change than more specialist or restricted species. There is evidence, however, that their distributions may still be strongly influenced by climate (Fuchs, Gilbert & Kamilar, 2017), and anthropogenic disturbance may also affect some populations even while others thrive in populous areas (e.g. chacma baboons; Stone, Laffan, Curnoe & Herries, 2015). We remain uncertain exactly how the different *Papio* species' ranges are delineated. Prior work has shown some *average* differences between species in the environments they occupy, but these are small and not systematic (Winder, 2015) – it is hard to predict whether specific taxa will be able to migrate to escape climate change, or whether their tolerances are sufficiently wide to permit persistence under changing conditions.

Species distribution models (SDMs) can be useful in addressing biogeographic and conservation-focused questions like these (Austin, 2002; Guisan et al., 2013). They can help identify zones of suitable but unused habitat and to predict how species' ranges will change in response to climate change (e.g. Chucholl, 2017; De Carvalho et al., 2017; Williams et al., 2009). The only prior study that models baboon ranges (Fuchs, Gilbert & Kamilar, 2017) focussed on evolutionary biogeography rather than predicting range shifts. The study was based on small samples of baboon localities and relatively few environmental variables, so it is possible that important constraints on *Papio* baboon niches/ranges were missed. This study builds on that work to consider whether (and how) baboon ranges are influenced by environmental variation, and how each species will be affected by future climate change. We are interested particularly in whether ecologically flexible, wide-ranging species like the baboons are likely to be less negatively affected by climate change or to suffer range loss, forced migration and increased extinction risk like their more specialist cousins.

## MATERIALS AND METHODS

### Data collection and processing

We used the software MaxEnt to produce our SDMs. This method has proven effective and reliable for a variety of taxa and, unlike some alternatives, can be run on incomplete datasets and using presence-only information (Phillips, Anderson & Schapire, 2006). It assumes only that the entire geographical area of interest is sampled (Kramer-Schadt et al., 2013) and the chosen environmental variables capture the species' biogeographical tolerances and hence their niche (Guisan, Theurillat & Kienast, 1998; Wiens, Stralberg, Jongsomjit, Howell & Snyder, 2009). MaxEnt uses locality points together with environmental data to characterise the species' niche and can then project it against maps of current and future conditions (Elith & Leathwick, 2009). Future projections assume additionally that the species' niche does not alter (Pearman et al., 2008), an assumption that seems reasonable when dealing with timescales of just 30-50 years for 2.5-6 degrees of warming.

Occurrence data for the six *Papio* species came from the Global Biodiversity Information Facility (GBIF, 2017) and the scientific literature. This provided a large dataset, but imposes some limitations of quality associated with editable online resources (Maldonado et al., 2015). Before using them we therefore imported all points obtained into ArcGIS 10.5.1 (ESRI, 2017) for cross-checking and quality control. We cross-checked all points against the IUCN (2017) Red List range maps for the species. Localities falling substantially outside of a species' IUCN range, or outside of Africa/Arabia, were discarded. The remaining points were checked for taxonomy and thinned out so a maximum of one point per pixel in the environmental layers remained. Final sample sizes ranged from 53 (*P. papio*) to 759 (*P. anubis*) with good geographic spread (Figure 1).

--- Figure 1 here ---

We also obtained maps of climatic conditions, vegetation and altitude (Table 1). Climatic conditions are important influences on primate distributions (Lehmann, Korstjens & Dunbar, 2010). Vegetation maps often enhance the predictive power of SDMs (Lewis et al., 2017) and altitude, although not having a direct effect on vertebrate physiology, has strong associations with many other factors like air pressure which do – its inclusion, although debated, seemed sensible here (Hof, Jansson & Nilsson, 2012). We obtained bioclimate maps from the WorldClim database (v. 1.4; Hijmans, Cameron, Parra, Jones & Jarvis, 2005) for current conditions (1950-2000) and two future periods, 2041-2060 (called '2050') and 2061-2080 ('2070') (Hijmans et al., 2005). These predicted future climatic conditions were drawn from three General Circulation Models (GCMs), namely MIROC-ESM, CCSM4 and HadGEM2-ES, all of which include atmosphere, ocean, land and sea-ice components and represent the products of long development in families of similar models (Watanabe et al., 2011; Gent et al., 2011; Martin et al., 2011). Including a range of models accounts for variability in future climate projections. Each model was run under two Representative Concentration Pathways (RCPs): RCP2.6 which represents a low-emission scenario and RCP6.0 which is one of the highest modelled assuming some action on climate change in the future (Wobus, Flanner, Sarofim, Moura & Smith, 2016). Altitude data was derived from the GTOPO30 elevation model (USGS, 1996) and vegetation data from WWF's Terrestrial Ecoregions of the World dataset (TEOW, Olson et al., 2001). All environmental datasets were converted to rasters with the same cell-size (30 arc seconds) in ArcGIS 10.5. The 'Clip' tools were used to ensure all maps aligned perfectly and data were exported as ASCII files for use in MaxEnt.

--- Table 1 here ---

### Species Distribution Modelling

We used MaxEnt 3.4.1 (Phillips, Dudik & Schapire, 2004) to build species distribution models (SDMs) for each *Papio* species under current environmental conditions. Each model used four-fold cross-validation replication to ensure all available data were used repeatedly for both training and testing of the model (Wenger & Olden, 2012). Variables making less than 1.5% contribution to the overall result were then removed, for ease of interpretation and to reduce overfitting, and the model repeated. Future distributions were projected using current conditions to train the model and future climatic maps matching the subset found to be important today. Model performance was assessed using the area under the receiver operating characteristic (ROC) curve (AUC), with an AUC of 0.9 or more considered an excellent model in line with prior studies (Mandrekar, 2010; Swets, 1988) and values of 1.0 potentially evidence of overfitting (Vidal-García & Serio-Silva, 2011).

Model outputs were exported to ArcGIS for further analysis and to produce categorised maps of habitat suitability under each RCP, GCM and projection year (2050 or 2070). Optimal and suitable distribution areas (those with a habitat suitability score >0.5 and >0.2 respectively) were extracted using the 'Zonal Geometry as Table' tool in ArcGIS 10.5.

## RESULTS

### Modelling current ranges and niches

Our SDMs demonstrated excellent general performance, with AUC values ranging from 0.946 (olive) to 0.979 (Guinea) and predicted ranges generally matching known distributions (Figure 2; c.f. Figure 1 for IUCN maps). They suggested that different species' distributions are differently affected by climatic and environmental variation. A maximum of 14 variables were deemed important (contributing >1.5%) to each SDM (Table 2), with different combinations for each species.

--- Table 2 here ---

Temperature and rainfall changed differently under different GCMs. Average values in the current ranges of each species showed that the CCSM4 and HadGEM2-ES models predicted warmer and drier conditions for all or most species by 2070, while MIROC-ESM predicted warmer and wetter ones for the northern species (Guinea, olive, yellow and hamadryas).

Both temperature and rainfall are important to the *Papio* species, in different ways. The southern taxa (yellow, kinda and chacma) were all most strongly affected by precipitation of the warmest quarter which contributed 41.4%, 40.2% and 21.7% to each SDM. For Guinea baboons the most important variable was altitude (39.6%) while for the olive it was annual precipitation (34.1%) and for the hamadryas, precipitation of the driest month (21.2%). We find different combinations of variables making up the top three or four (>10% contribution) for different species (Table 2), with some common themes. Vegetation is important to Guinea and olive baboons (contributing 25.9% and 12.8% respectively); altitude also matters for hamadryas (13.2%) and temperature annual range to hamadryas (18%) and yellow (12.8%). Annual mean precipitation contributed 12.8% to the hamadryas model and 11.4% to the yellow baboon model and mean temperature of the coldest quarter contributed 21% for olive and 16.7% for chacma models. Other important variables were different for each species: annual mean temperature was significant for Guinea baboons (11.5%); precipitation of the wettest and driest quarters for kinda (14.7% and 22.6% respectively) and temperature of the driest quarter and temperature seasonality to chacma (21.1% and 18% respectively).

Predicted areas of high habitat suitability were close to what we'd expect for the various species (see Figure 2 and cf. Figure 1). However, our models did identify some apparently highly suitable areas where we do not think the species are found. These include areas of optimal Guinea baboon habitat slightly to the east of their known IUCN range and for the hamadryas baboon more northwards along

the coast either side of the Red Sea. The IUCN range for chacma baboons excludes parts of Botswana; their predicted potential distribution here suggests this area includes some areas of high habitat suitability. Although localities far outside the species' IUCN ranges were excluded, the yellow and chacma baboon SDMs predicted some optimal areas quite a long way away too. This occurs for the yellow baboon along parts of the south-west border within Angola and further up the coast in Ghana, Togo and Benin and for the chacma baboon in Madagascar and Yemen. These areas may be unoccupied due to barriers to dispersal or conflict with local human populations, or they may be occupied and not included in the IUCN maps for reasons presumably to do with low population density and/or gaps in available data.

--- Figure 2 here ---

These models confirmed that different baboons have differently sized suitable and optimal ranges (Table 3). The area of predicted suitable habitat (scoring  $>0.2$  in the MaxEnt model) is largest for the chacma baboon at  $\sim 3,774,538\text{km}^2$  and smallest for the kinda at  $\sim 839,494\text{km}^2$ . Focusing specifically on areas of moderate-high habitat suitability (scoring  $>0.4$ ), our predicted distributions for olive and kinda baboons are substantially smaller than their IUCN ranges (Table 3). Our predicted distribution for the olive baboon comprises four separate areas scoring  $>0.4$  collectively covering  $\sim 1,043,404\text{km}^2$ . These are spread across the IUCN range which is eight times larger ( $\sim 8,356,442\text{km}^2$ ), and surrounded by either barely suitable or unsuitable areas. The kinda baboons' predicted reasonably suitable distribution ( $>0.4$ ) covering  $\sim 446,070\text{km}^2$  occurs mostly on the east side of the IUCN range ( $\sim 2,378,787\text{km}^2$ ), which is nearly five and a half times larger than the predicted suitable area.

--- Table 3 here ---

### Impacts of climate change

Twelve potential future distributions were predicted for each baboon species, using three GCMs (CCSM4, HadGEM2-ES and MIROC-ESM) each for RCP2.6 and RCP6.0 and 2050 and 2070. The outputs reveal that if the variables which currently limit the ranges of *Papio* spp. continue to do so, the distributions of each species will change in future, some of them substantially ( $>\pm 25\%$ ; Table 4). In particular, the Guinea, chacma and kinda baboons may see substantial range losses by 2070, and seem to do so consistently across two or more of the climate models and scenaria used (Figures 3-5). In contrast, the olive and hamadryas baboons are typically predicted to experience a substantial increase in the area of suitable habitat (Figures 7-8), while the yellow baboon's predicted range changes vary depending on the model and scenario chosen, but often not substantially (see Table 4 and Figure 6).

--- Table 4 here ---

---Figures 3-8 somewhere here ---

### Baboons 'at risk'

The chacma baboon (*P. ursinus*) is predicted to be at greatest risk from climate change. All future predictions of the chacma range show a substantial decrease in optimal habitat by 2070 under both RCPs and all but two (CCSM4, RCP2.6, 2050 and 2070) also predict a substantial loss of habitat overall too. Even these predict range contractions of over 20% (Table 4 and Figure 3). Under RCP2.6, the species' optimal range is predicted to reduce by 42.84-59.54% by 2050 and 40.95- 57.41% by 2070. Under RCP6.0, the decline in optimal habitat is predicted to be 54.02-58.69% by 2050 and 59.02-65.41% by 2070. These habitat losses may include something of a southward range shift (Figure 3).

The Guinea baboon (*P. papio*) is also at risk. Under all models based on CCSM4 and HadGEM2-ES it is predicted to have significantly less optimal habitat available (Table 4, Figure 4). Under RCP6.0 in

2070 this species is predicted an 82.99-86.49% decline in optimal habitat by these models, though predictions from MIROC-ESM predict an increase of 49.19% under RCP2.6 and 32.15% under RCP6.0. Overall suitable habitat is also expected to decline under the CCSM4 and HadGEM2-ES models, though not always substantially (for HadGEM2-ES, the decline is predicted to be just 4.94% in 2050 under RCP2.6 and 7.62% in 2070). The MIROC-ESM models, however, predict substantial increases of 42.27-79.67% in broader suitable habitat. If ongoing anthropogenic changes follow the pattern predicted by CCSM4 or HadGEM2-ES, which both predict warming and drying, the Guinea baboon will thus be the worst affected baboon species by 2070, but if they follow the wetter scenario envisioned by MIROC-ESM it may do better and even expand its range substantially, especially to the east (Figure 4).

The third vulnerable species is the kinda baboon which is most threatened under the MIROC-ESM model (Table 4, Figure 5). For 2050, this species will suffer a 44.82-49.78% loss of optimal habitat if MIROC-ESM is accurate, and the same model predicts 36.52-75.40% loss by 2070. Under drier scenarios, however, the species may experience no major changes in optimal habitat, or even a small increase of 11.12-12.61% under the HadGEM2-ES model and RCP6.0 (Table 4). Predictions for the impact on suitable habitat are similarly varied, with MIROC-ESM predicting a loss of 25.88-46.52% and other models predicting anything from stasis, especially in 2050 and under RCP2.6, to a 33.58% increase by 2070 under RCP6.0. Maps suggest the kinda distribution may consolidate in the central parts of its current range or fragment, depending on the precise nature of ongoing climate change (Figure 5).

#### **‘Resilient’ species**

The yellow baboon, *P. cynocephalus*, is predicted to experience no substantial (>25%) changes in either its optimal range or its overall range (Table 4, Figure 6). Predictions for the optimal habitat zone range from a loss of 24.69% under MIROC-ESM and RCP6.0 in 2050, to a gain of 5.02% under the CCSM4 model and RCP2.6 in 2070. Total suitable habitat areas are predicted to increase by 1.57-17.10% except under the CCSM4 model and RCP6.0, which predicts a decline of 10.44% in 2050 and 13.18% by 2070. This species’ predicted future range often includes parts of west Africa which the species would have to travel long-distance to actually colonise (Figure 6).

#### **Beneficiaries of changing climates**

The remaining two baboon species, olive (*P. anubis*) and hamadryas (*P. hamadryas*) are predicted to increase both their optimal and suitable ranges under future climatic conditions, irrespective of the RCP, GCM or year modelled. The amount of increase varies (Table 4, Figures 7-8). For the olive baboon the area of optimal habitat is predicted to increase by 61.65-231.96%, with the greatest increases under the HadGEM2-ES model and the MIROC-ESM model for RCP6.0. The area of suitable habitat is predicted to increase by 24.38-80.22% in a similar pattern (Table 4). This species seems likely to expand its range quite substantially as climates warm, by linking up existing areas of optimal habitat and perhaps moving south to encroach on the yellow baboon range (see Figure 7).

For the hamadryas baboon the picture is similar. Our models predict an increase of 46.85-187.62% in optimal habitat, especially under the HadGEM2-ES model for RCP6.0 and 2070 and the MIROC-ESM model for the same scenario and year. Total suitable habitat is predicted to increase by 72.94-224.89%, mostly through expansion into southern Arabia and south along the African rift (Table 4, Figure 8).

## **DISCUSSION**

This study has demonstrated that MaxEnt can be used to predict baboons’ biogeographic responses to climate change. Our SDMs reached high levels of accuracy ( $AUC \geq 0.946$ ). Predictions of the species’

ranges under 12 different climate change scenarios has shown, furthermore, that the *Papio* baboons, despite their large ranges and ecological flexibility, cannot be treated as uniformly at low risk from climate change. The chacma, Guinea and kinda baboons likely face significant losses of optimal and/or suitable habitat, while closely-related olive and hamadryas baboons may expand their ranges and yellow ones will probably not change theirs very much. These results suggest, to us, that biogeographers might usefully take more of an interest in climate change effects on seemingly resilient species – if some baboons are potentially threatened, other mammals now considered Least Concern might well be too. We also found a lot of variation in our SDM predictions for each species, which may be informative about their prospects under different degrees and types of climate change.

### **SDMs, environmental controls on distributions and current ranges**

Our predictions suggest that baboons, despite being behaviourally flexible, seem to be subject to some environmental limits on their ranges. Each species' potential range contains some patches of optimal habitat (suitability >0.5; Figure 2). These optimal areas are approximately 41% (Guinea), 23% (olive), 49% (hamadryas), 42% (yellow and kinda) and 32% (chacma) of their total suitable habitat area (>0.2). The olive baboons' optimal habitat percentage may be lower because it is the most widespread species. SDMs for wide-ranging species may produce less accurate results due to the increased risk of omission error (Gonzalez, Soto-Centeno & Reed, 2011; Hernandez, Graham, Master & Albert, 2006). This may also explain why this species' SDM predicts a range substantially smaller than its IUCN map, though SDMs can also appear like this if they are constructed from too few locality points or with biased localities (Kramer-Schadt et al., 2013). Our samples were quite large and well-spread (see Figure 1), but further sampling could confirm whether population density varies across the species' range in accordance with our results or whether an SDM with more localities is more accurate.

In fact, all our current SDMs predict some areas of optimal habitat outside the species' IUCN ranges (Figure 2). For the hamadryas baboon, these include parts of the Arabian coast northwards of the IUCN range where the species may already live (Winney et al., 2004), and the same could be true for other species and instances – baboon range maps in the literature do vary, and there will always be challenges associated with mapping ranges over such large areas. Alternatively, these areas may be too distant to colonise. Madagascar and parts of Arabia, for instance, are predicted to be suitable for chacma baboons but we presume are not used by them due to distance and intervening biogeographic barriers; the east coast of Angola is similarly distant from the yellow baboon range and presumably unoccupied. Our SDMs also predict that the chacma baboon might be found in parts of Botswana outside their IUCN range, where there are no clear barriers to dispersal. If they are indeed not found here, factors limiting their spread might include physical inaccessibility (e.g. electric fences: Hoffman & O'Riain, 2012); isolation from other optimal habitat areas; conflict with humans; or the region having a very low carrying capacity (e.g. low food and water availability; Altmann, 1974). This third suggestion is supported by the fact that this area includes parts of the Kalahari Desert. There has been a report of a solitary male chacma baboon crossing the Central Kalahari Game Reserve (Hamilton & Tilson, 1982). While this suggests baboons can survive here temporarily, it does not show that the area could support permanent occupation.

The SDMs also suggest each species has adapted to a distinct niche: we found relatively little overlap in species' predicted optimal distributions. Some of the modelled areas of overlap are established hybrid zones, for instance between the olive and hamadryas baboons (Bergman, Phillips-Conroy & Jolly, 2008) and the olive and yellow baboons (Alberts & Altmann, 2001). Interspecific competition may limit some overlaps (Connor & Bowers, 1987), but there may also be demographic and phylogenetic shifts among baboons in future (e.g. speciation and reticulation events) as different populations come into and move out of contact. Baboons seem particularly prone to reticulation, hybridising across genus boundaries in

places (Winder & Winder, 2014). Minimal areas of habitat suitability were predicted within other species' distributions for pairs which do not hybridise in the wild, which might suggest they are unable to live within each other's ranges, perhaps because of past competition (Connell, 1980).

Our models build on the results of earlier SDM studies (Fuchs et al., 2017) in several ways. We used larger samples of localities (53-759 cf. 8-86); incorporated more environmental variables including vegetation and altitude; and projected ranges across the whole of Africa rather than just the species' combined current ranges. Our higher AUC values (0.946-0.979 compared to 0.762-0.949 in Fuchs et al.'s study) suggest these changes have improved the results, but our specific findings also corroborate and extend upon theirs. Most of our areas of optimal habitat appear to coincide with theirs, suggesting these are reliably attractive for the species concerned. We do, however, find some differences in the variables that contribute most to our SDMs. For three species (hamadryas, kinda and chacma) Fuchs et al.'s most important variables appeared in the top three or four in our models too, but for two (olive and yellow) our models did not include their top predictors because they were found to contribute less than 1.5%. Fuchs et al.'s top variable for the Guinea baboon did not seem very important in our SDM, where it contributed just 2.4%. Many of the higher ranked variables identified here were not included in Fuchs et al.'s study.

### **Responses to climate change**

We incorporated multiple scenarios for future climate change and found that different models predicted different threat levels for each species. Our current SDMs suggested that all six *Papio* species are influenced by both temperature and rainfall in different ways. This is replicated in the predictive models, with the three GCMs sometimes predicting different biogeographic changes (e.g. in some cases, one or two models predict range loss while others predict stability or expansion). In particular, the CCSM4 and HadGEM2-ES models predicted the greatest threat to the Guinea baboon, potentially because they predict warmer and drier conditions while the MIROC-ESM model predicts warmer but considerably wetter conditions. Five rainfall-linked variables contributed to the Guinea baboon's current SDM, strongly suggesting this species prefers wetter to drier conditions and will be especially affected by changes to precipitation. The same is true for the kinda baboon the opposite way around – for this species, the MIROC-ESM predictions were the worst-case scenarios, suggesting it is near the upper limit of its tolerance for precipitation. Precipitation may affect baboon distributions directly or indirectly via effects on vegetation and competition, and the effects can be severe: we know some species show reduced conception rates during or after a drought, for instance (Beehner, Onderdonk, Alberts & Altmann, 2006; Bercovitch & Harding, 1993; Lycett, Weingrill & Henzi, 1999).

The chacma baboon was the only species for which every modelled scenario predicted a loss of suitable and optimal habitat. This species is sensitive to the amount of precipitation in the warmest quarter of the year, which may be especially affected by climate change, and may be particularly badly affected because it cannot move polewards to track suitable conditions. Our models thus suggest this is the species at greatest risk of range loss and hence possibly extinction, though that risk depends also on its adaptability and potential to disperse (Berg et al., 2010). We would argue that behavioural change might mitigate or exacerbate the impacts of environmental shifts for particular species, with baboons possibly able to exercise some element of agency or innovation to find new ways of being fit under changing conditions (see, for instance, the arguments in Winder & Winder, 2015).

Yellow baboons do not appear likely to be much affected by climate change under our models, seeing predicted ranges increasing by up to 5.02% or decreasing by up to 18.77%. Interestingly the yellow baboons' 2070 predicted distribution for the models MIROC-ESM and HadGEM2-ES (RCP6.0) is split into two fragments (Figure 6). If this does happen, it could possibly drive genetic separation in the populations on either side (Qvarnström, Ålund, McFarlane & Sirkiä, 2016).

Changes in climate are known to negatively influence many species' distributions (McCarty, 2001), but for two species studied here (olive and hamadryas) we predict the opposite. Both species' optimal habitat areas are predicted to increase by 2070 by 80.30-231.96% (olive) and 46.85-187.62% (hamadryas) for both RCPs. However, these predictions do not guarantee occupancy across the whole newly suitable area because other factors may limit their dispersal, for instance geographical barriers (Harcourt & Wood, 2012; Vences, Wollenberg, Vieites & Lees, 2009).

### **Model limitations**

All SDMs are subject to uncertainties, and our predictions may overestimate the true range of the species (Amboni & Laffan, 2012). This might occur because of factors not incorporated into the models like anthropogenic impacts, interspecific competition, geographical barriers, predation, food and water availability and other threats, such as fires (e.g. Gonzalez et al., 2011; McPherson & Jetz, 2007). Therefore, even if a species' suitable habitat area is predicted to increase it should not be assumed that the species will disperse to cover the whole area. To overcome this, additional important variables which may influence baboon distributions could be included, or further smaller-scale analysis of the variation in population dynamics and dispersal could be incorporated, both aimed at improving accuracy in future generations of SDMs. In particular, we were unable to use future vegetation maps, which do not yet exist because it is hard to predict how vegetation zones will shift in response to environmental change (Tang & Bartlein, 2008). This would most probably have affected those SDMs (for Guinea, olive, hamadryas and chacma) for which vegetation was important. We would also suggest prioritising models using only the most recent locality data, and, depending on the progress of future climate change talks, assessing how baboon ranges might change under the most severe emissions scenario, RCP8.5, which will arise if only minimal efforts are made to reduce emissions (Riahi et al., 2011). This would be a particular priority for the chacma, Guinea and kinda baboons.

These models can be seen as provisional attempts to characterise the impacts of climate change on baboons. The large sample sizes, good range of variables and use of multiple climate change scenarios may provide a robust starting point for future research and conservation. Monitoring species' distributions is a key part of conservation (McCarty, 2001). Our models suggest that it may be time to update the IUCN range maps for certain baboon species via targeted investigations of areas of predicted habitat suitability that lie outside their currently recognised range boundaries. We can also use them to identify proposed priority conservation areas for the three species predicted to suffer the worst range losses as climate changes (Figure 9). These are zones which are predicted to be highly suitable or optimal for the species in future, under more than one model of climate change; updating our SDMs periodically as described above will hopefully confirm their utility. We hope that these results will encourage effective management plans (Villero, Pla, Camps, Ruiz-Olmo & Brotons, 2017) specific to the species of the proposed priority areas, so that conservation efforts can be better targeted.

--- Figure 9 here ---

### **Conclusion**

We aimed to evaluate the impact of environmental variation and climate change on the biogeography of the six *Papio* species by modelling their ranges under current conditions and future climate change scenarios. Our analysis has confirmed previous findings that there are differences in the environmental conditions occupied by each species. Further exploration also suggested that three of six baboon species, despite being relatively wide-ranging and flexible, will suffer significant declines in their potential range while two may benefit and one is likely to experience only small shifts. Effective conservation strategies will be required to mitigate the effects of climate change particularly for the Guinea baboon – which will suffer almost complete range loss if warmer temperatures make the region drier – and the

chacma baboon, whose ability to migrate is limited. Overall, we have shown that the biogeography of *Papio* is complex and simply characterising these species as ecologically 'resilient' or 'flexible' may obscure potent risks to their future. More investigation of other mammal and primate species in the IUCN's Least Concern category is thus warranted to check whether this generalises beyond *Papio*.

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## DATA ACCESSIBILITY

The environmental data and localities used in this study came from publicly available sources which are fully referenced in the text. Our SDM outputs for current and future predicted ranges will be available from DRYAD (DOI to follow).

## BIOSKETCH

Sarah E. Hill conducted this work during the fourth year of her Masters in Zoology with Animal Behaviour at Bangor University. She is broadly interested in the ecology and behaviour of the mammals, with especial focus on distribution modelling and responses to climate change. Isabelle C. Winder is a Lecturer in the School of Biological Sciences at Bangor, with research interests focusing on primate (including human) evolution, ecology and morphology and especially the role of complex evolutionary processes incorporating primate agency and ecological/behavioural flexibility.

Author contributions: ICW and SEH conceived the ideas; SEH collected and analysed the data; SEH and ICW wrote the text.

## TABLES

**Table 1.** Environmental variables used in SDMs for the six *Papio* species and their sources.

Category	Variable	Time period	Source
<b>Species' occurrence records</b>	Coordinates (longitude and latitude) for the known locations of the Guinea, olive, hamadryas, yellow, kind and chacma baboons	Current	GBIF and literature (including Science Direct, Google Scholar and Nature)
<b>Species' distributions</b>	Range maps for the Guinea, olive, hamadryas, yellow, kind and chacma baboons	Current	The IUCN Red List (IUCN, 2017)
<b>Climatic conditions</b>	Annual Mean Temperature (Bio1)	Both	WorldClim database (Hijmans et al., 2005)
	Mean Diurnal Range (Bio2)	Both	
	Isothermality (Bio3)	Both	
	Temperature Seasonality (Bio4)	Both	
	Max Temperature of Warmest Month (Bio5)	Both	
	Min Temperature of Coldest Month (Bio6)	Both	
	Temperature Annual Range (Bio7)	Both	
	Mean Temperature of Wettest Quarter (Bio8)	Both	
	Mean Temperature of Driest Quarter (Bio9)	Both	
	Mean Temperature of Warmest Quarter (Bio10)	Both	
	Mean Temperature of Coldest Quarter (Bio11)	Both	
	Annual Precipitation (Bio12)	Both	
	Precipitation of Wettest Month (Bio13)	Both	
	Precipitation of Driest Month (Bio14)	Both	
	Precipitation Seasonality (Bio15)	Both	
	Precipitation of Wettest Quarter (Bio16)	Both	
	Precipitation of Driest Quarter (Bio17)	Both	
	Precipitation of Warmest Quarter (Bio18)	Both	
	Precipitation of Coldest Quarter (Bio19)	Both	
<b>Vegetation</b>	Vegetation map	Current	TEOW (Olson et al., 2001)
<b>Altitude</b>	Altitude	Current	GTOPO30 (USGS, 1996)

**Table 2.** Variables having an important (>1.5%) effect on the range of each baboon species under current climatic conditions, in order of importance and with contributions in brackets. Variables making more than a 10% contribution are highlighted in **bold** text.

Species	Important variables, in order of percentage contribution to the model
Guinea baboon ( <i>P. papio</i> )	<b>Altitude (39.2%)</b> , <b>vegetation (25.9%)</b> , <b>annual mean temperature (11.5%)</b> , precipitation of driest month (3.7%), precipitation of coldest quarter (3.6%), precipitation of warmest quarter (3.3%), precipitation of wettest quarter (3.2%), mean temperature of warmest quarter (2.8%), precipitation of driest quarter (2.4%), isothermality (2.3%) and temperature annual range (1.9%).
Olive baboon ( <i>P. anubis</i> )	<b>Annual precipitation (34.1%)</b> , <b>mean temperature of coldest quarter (21%)</b> , <b>vegetation (12.8%)</b> , mean temperature of warmest quarter (8%), minimum temperature of coldest month (5.1%), precipitation of warmest quarter (4.8%), annual mean temperature (4.4%), temperature annual range (2.7%), isothermality (2.2%), precipitation of driest month (2.2%), precipitation of coldest quarter (1.8%) and altitude (0.9%).

Hamadryas baboon ( <i>P. hamadryas</i> )	<b>Precipitation of driest month (21.1%), temperature annual range (18%), altitude (13.2%), annual precipitation (12.8%),</b> vegetation (7.1%), annual mean temperature (6.1%), temperature seasonality (5.4%), isothermality (3.5%), precipitation of coldest quarter 2.8%), precipitation of warmest quarter (2.6%), precipitation of driest quarter (2.3%), precipitation of wettest quarter (2.2%), mean temperature of coldest quarter (1.6%) and mean temperature of driest quarter (1.4%).
Yellow baboon ( <i>P. cynocephalus</i> )	<b>Precipitation of warmest quarter (41.4%), temperature annual range (12.8%), annual precipitation (11.4%),</b> temperature seasonality (9.9%), precipitation of coldest quarter (9.1%), mean diurnal range (8.3%), precipitation of driest month (5.3%) and minimum temperature of coldest month (1.9%).
Kinda baboon ( <i>P. kindae</i> )	<b>Precipitation of warmest quarter (40.2%), precipitation of driest quarter (22.6%), precipitation of wettest quarter (14.7%),</b> precipitation of coldest quarter (7.5%), precipitation of driest month (6.7%), mean diurnal range (3%), temperature annual range (2.2%), temperature seasonality (2.1%) and precipitation of wettest month (1%).
Chacma baboon ( <i>P. ursinus</i> )	<b>Precipitation of warmest quarter (21.7%), mean temperature of driest quarter (21.1%), temperature seasonality (18%), mean temperature of coldest quarter (16.7%),</b> isothermality (7.8%), altitude (6.4%), annual mean temperature (4.4%) and vegetation (3.8%).

**Table 2.** The predicted suitable and optimal habitat areas under current climatic conditions for each of the six baboon species and their estimated IUCN range size.

Species	Predicted habitat area (km <sup>2</sup> )		Estimated IUCN range area (km <sup>2</sup> )
	Suitable area (>0.2)	Optimal area (>0.5)	
<b>Guinea</b>	935,609	385,905	442,439
<b>Olive</b>	2,910,865	681,315	8,356,442
<b>Hamadryas</b>	911,327	450,909	612,368
<b>Yellow</b>	2,644,487	1,099,318	1,949,618
<b>Kinda</b>	839,494	349,026	2,378,787
<b>Chacma</b>	3,774,538	1,216,805	3,386,086

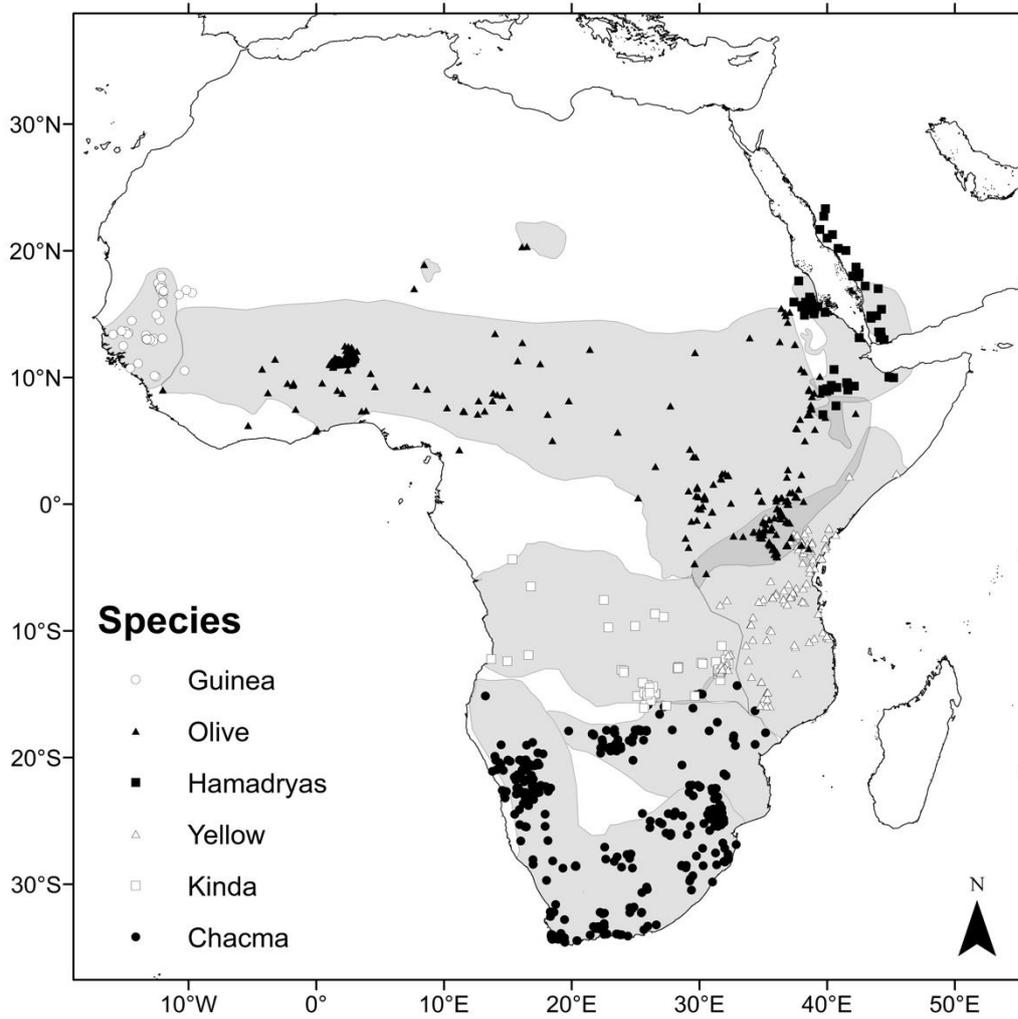
**Table 4.** The estimated area of habitats of differing degrees of suitability for each baboon species and model/scenario, together with percentage differences from current conditions. Each species' future range has been modelled twelve times, for three models (C=CCSM4; H=HadGEM2-ES; M=MIROC-ESM) each under two RCPs (2.6 and 6.0) and in two different periods, 2050 and 2070. In the final two columns, dark grey shading indicates an area more than 25% less than the equivalent prediction today, light grey a model predicting a small change in area (less than  $\pm 25\%$ ) and white a model predicting an area more than 25% more than today's. The four classes of habitat suitability used are 0.2-0.4 indicating barely suitable habitat, 0.4-0.5 indicating suitable habitat, 0.5-0.75 indicating highly suitable habitat and 0.75-1 indicating ideal habitat.

Species	Year	Model	RCP	Estimated area (km <sup>2</sup> )				Difference with present (%)	
				0.2-0.4	0.4-0.5	0.5-0.75	0.75-1	>0.2	>0.5
Guinea	-	Present	-	460295.15	89408.58	209997.61	175907.74	-	-
	2050	C	2.6	398886.06	97275.95	98163.40	48936.48	-31.25	-61.88
		H	2.6	512031.15	150540.50	156749.16	70091.12	-4.94	-41.22
		M	2.6	810386.81	296154.53	257357.84	119602.20	69.25	-2.32
		C	6.0	381549.98	57160.79	68566.08	28005.79	-42.79	-74.98
		H	6.0	439293.07	88406.34	82488.14	17485.86	-32.91	-74.09
		M	6.0	747549.97	180436.68	260362.55	142710.92	42.27	4.45
	2070	C	2.6	407477.82	97556.61	107469.04	47538.81	-29.45	-59.83
		H	2.6	507027.70	138599.81	145583.93	73090.82	-7.62	-43.33
		M	2.6	753310.01	256945.02	389716.21	186005.64	69.51	49.19
		C	6.0	198579.73	34042.98	39825.41	12312.33	-69.56	-86.49
		H	6.0	407509.32	79550.03	55577.66	10069.91	-40.93	-82.99
		M	6.0	932729.75	238261.66	301386.85	208600.65	79.67	32.15
	Olive	-	Present	-	1867460.17	362089.69	477688.97	203625.97	-
2050		C	2.6	2200756.52	568033.85	844033.14	603134.89	44.84	112.41
		H	2.6	2335935.45	583869.60	1125062.49	805338.43	66.62	183.33
		M	2.6	2050713.81	468510.62	688150.43	413220.66	24.38	61.65
		C	6.0	2397535.74	607922.53	916081.41	541637.00	50.24	113.96
		H	6.0	2369068.00	630247.26	1168301.33	746053.58	68.80	180.98
		M	6.0	2127957.34	581650.11	939084.13	1039571.75	61.06	190.42
2070		C	2.6	2247716.71	574768.50	880305.62	626850.98	48.74	121.21
		H	2.6	2203725.87	634748.47	1189185.38	811121.55	66.23	193.60
		M	2.6	2154029.12	521578.95	753149.74	475250.64	34.12	80.30
		C	6.0	2363681.78	650050.01	1037753.44	619402.97	60.46	143.23
		H	6.0	2392763.68	800366.28	1366761.00	686028.55	80.22	201.30
		M	6.0	2149358.44	755959.25	1266137.14	995546.60	77.51	231.96
Hamadryas		-	Present	-	350887.83	109530.54	219893.41	231015.20	-
	2050	C	2.6	845701.79	139158.99	255093.20	420115.61	82.16	49.74
		H	2.6	1119340.70	292692.90	401339.36	508819.44	154.81	101.85
		M	2.6	730815.03	151832.92	267168.97	426222.47	72.94	53.78
		C	6.0	971748.44	216032.15	283609.76	457816.96	111.69	64.43
		H	6.0	1128638.96	277721.64	418782.22	537129.95	159.21	112.00
		M	6.0	744563.64	202873.52	413984.23	425306.62	96.06	86.13
	2070	C	2.6	837936.59	132048.24	258755.69	403387.08	79.09	46.85
		H	2.6	1132020.96	312000.14	426752.55	532632.40	163.73	112.77
		M	2.6	860595.89	203380.92	352816.65	442514.40	104.02	76.38
		C	6.0	1160364.14	242220.50	307757.65	509872.35	143.62	81.33
		H	6.0	1283422.73	380524.45	596152.69	700737.28	224.89	187.62
		M	6.0	1041409.18	382368.86	479761.01	670167.56	182.41	155.02
	Yellow	-	Present	-	1221218.57	323950.64	610956.93	488361.27	-
2050		C	2.6	1222172.56	334614.06	656416.22	472710.16	1.57	2.71
		H	2.6	1491554.44	385673.72	592366.76	337764.61	6.16	-15.39
		M	2.6	1514427.04	376574.24	575163.52	444181.80	10.05	-7.27
		C	6.0	1076370.26	320082.11	632049.58	339960.28	-10.44	-11.58
		H	6.0	1469073.96	371394.12	668992.11	335764.99	7.59	-8.60
		M	6.0	1474054.39	385909.72	557404.78	270544.62	1.64	-24.69
2070		C	2.6	1240331.59	331017.83	660136.80	494412.76	3.08	5.02

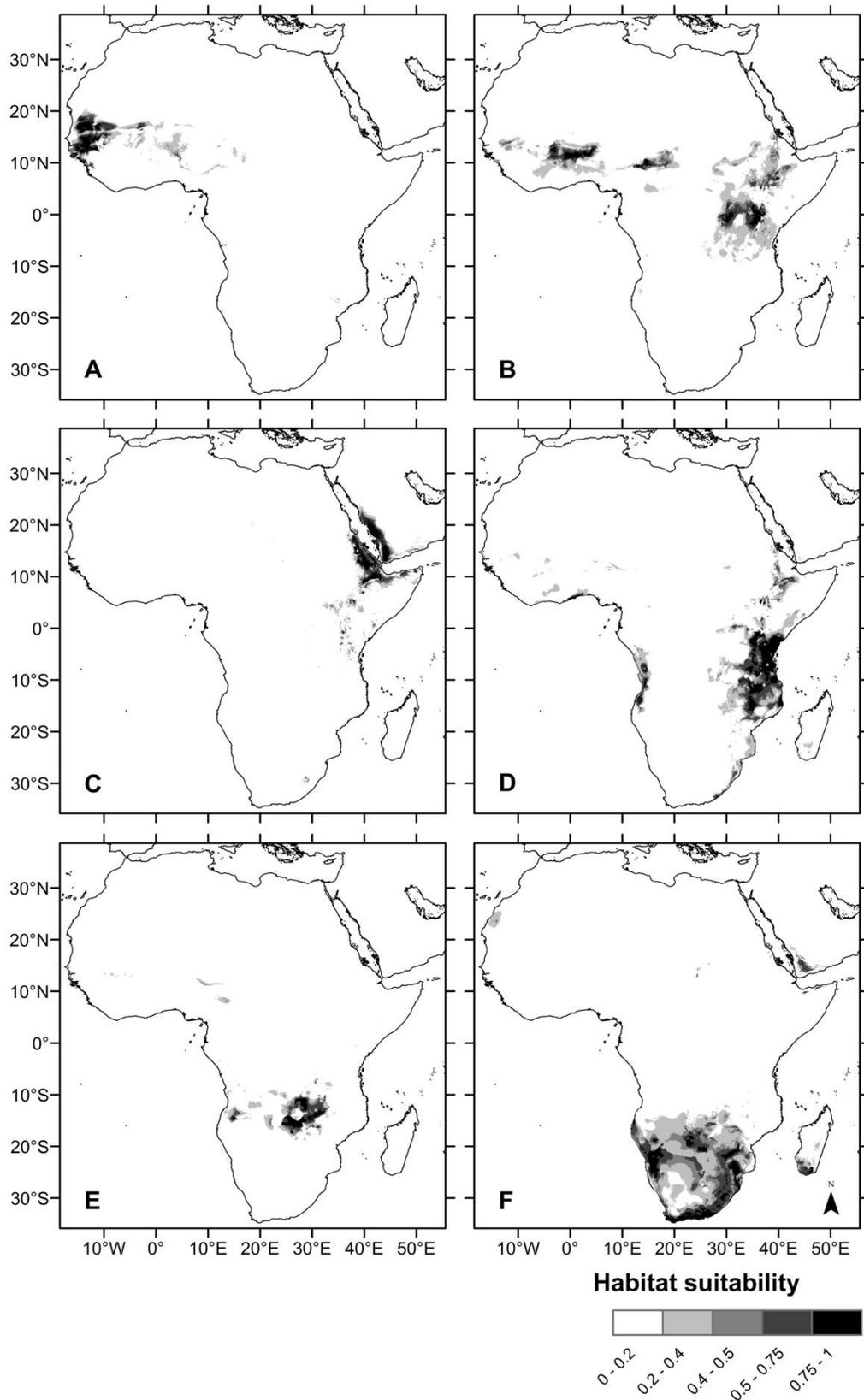
	H	2.6	1434990.61	396992.48	577373.72	315648.10	3.04	-18.77	
	M	2.6	1545312.63	397816.65	662316.13	491300.33	17.10	4.94	
	C	6.0	1000585.41	319866.08	628915.36	346623.55	-13.18	-11.26	
	H	6.0	1520660.07	418486.32	656744.80	312027.37	9.96	-11.88	
	M	6.0	1585273.21	442056.02	726579.81	245903.86	13.44	-11.54	
	- Present	-	393423.49	97044.68	203583.83	145441.97	-	-	
Kinda	2050	C	2.6	423752.51	96301.90	219737.46	150284.61	6.03	6.02
		H	2.6	489504.38	134542.80	252068.44	140453.79	21.09	12.46
		M	2.6	289410.23	68316.58	133708.38	58900.81	-34.44	-44.82
		C	6.0	457201.44	83254.16	164274.58	148266.48	1.61	-10.45
		H	6.0	555415.81	106639.40	200944.74	192076.63	25.68	12.61
		M	6.0	361802.95	70824.14	111637.28	63632.41	-27.59	-49.78
	2070	C	2.6	407049.07	76385.84	225999.90	208449.11	9.34	24.47
		H	2.6	468963.06	94386.19	203415.65	144813.46	8.59	-0.23
		M	2.6	308364.66	92295.84	135752.38	85798.38	-25.88	-36.52
		C	6.0	450335.28	81301.79	193548.18	154551.57	4.79	-0.27
		H	6.0	623710.83	109830.46	198072.79	189767.43	33.58	11.12
		M	6.0	306281.85	56796.44	59289.99	26556.90	-46.52	-75.40
	- Current	-	1860657.00	697075.95	835658.24	381146.56	-	-	
Chacma	2050	C	2.6	1690580.28	458765.69	542980.40	152495.71	-24.63	-42.84
		H	2.6	1427709.70	428343.97	406020.60	128350.43	-36.67	-56.08
		M	2.6	1344549.34	410613.14	372224.54	120054.77	-40.46	-59.54
		C	6.0	1426454.85	421251.42	437425.53	122037.32	-36.23	-54.02
		H	6.0	1211457.61	407257.13	415558.19	111887.39	-43.14	-56.65
		M	6.0	1253744.47	328986.85	384810.87	117867.38	-44.75	-58.69
	2070	C	2.6	1777503.09	458528.52	556031.38	162466.67	-21.72	-40.95
		H	2.6	1405481.22	426796.95	430350.23	130237.03	-36.61	-53.93
		M	2.6	1363596.48	455616.68	397705.53	120490.30	-38.07	-57.41
		C	6.0	1338356.98	414503.85	398615.42	100024.44	-40.35	-59.02
		H	6.0	1042530.13	272084.75	343430.68	77450.97	-54.02	-65.41
		M	6.0	915234.06	245088.00	412978.39	75211.84	-56.33	-59.88

## FIGURES

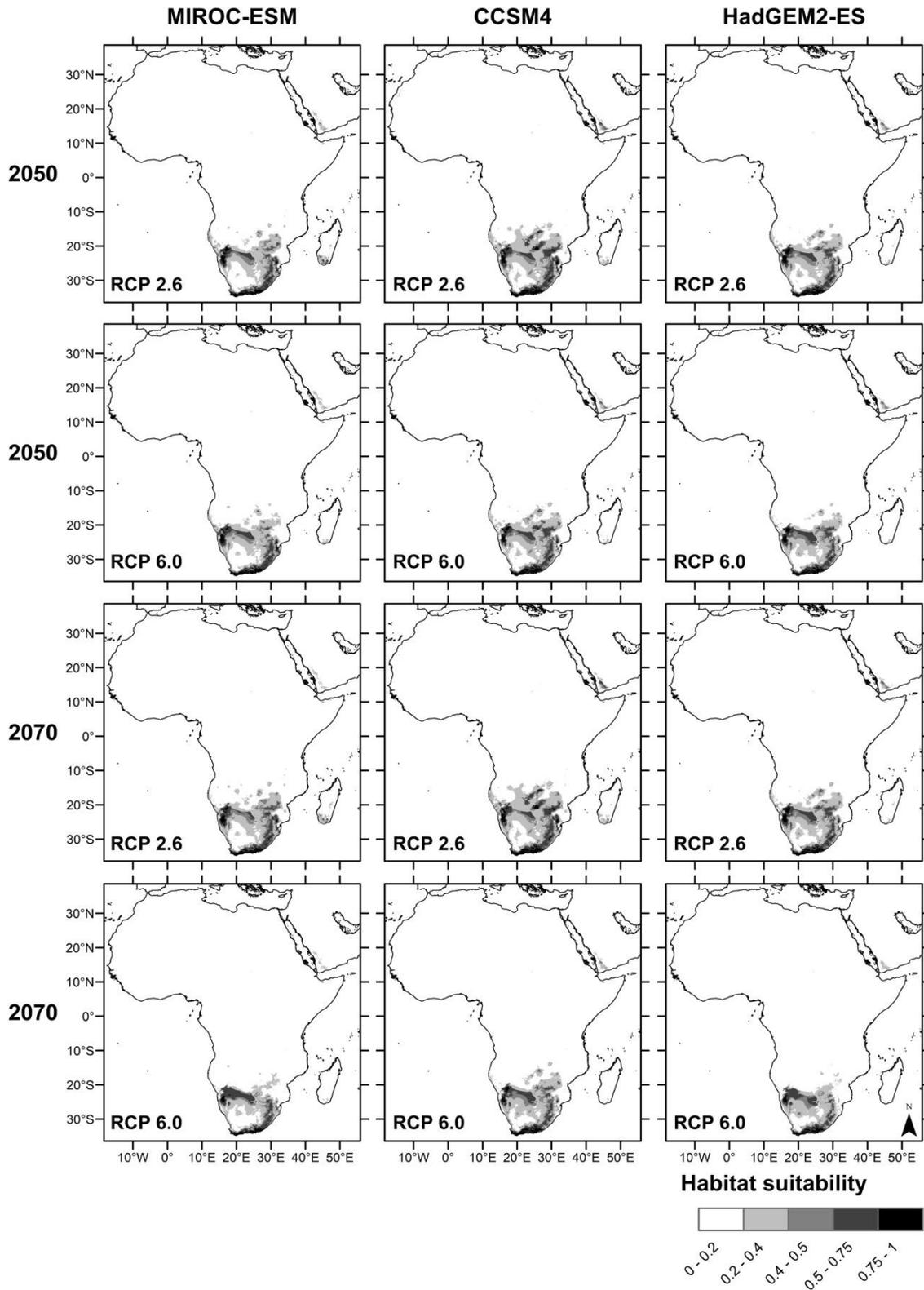
**Figure 1.** Localities from the GBIF (2017) and georeferenced scientific papers, shown overlain on the IUCN (2017) range maps for each of the six *Papio* baboon species whose distributions are modelled in this paper. Final sample sizes from 53-759 (*P. papio*: 53; *P. hamadryas*: 58; *P. cynocephalus*: 132; *P. kindae*: 76; *P. anubis*: 759 and *P. ursinus*: 353).



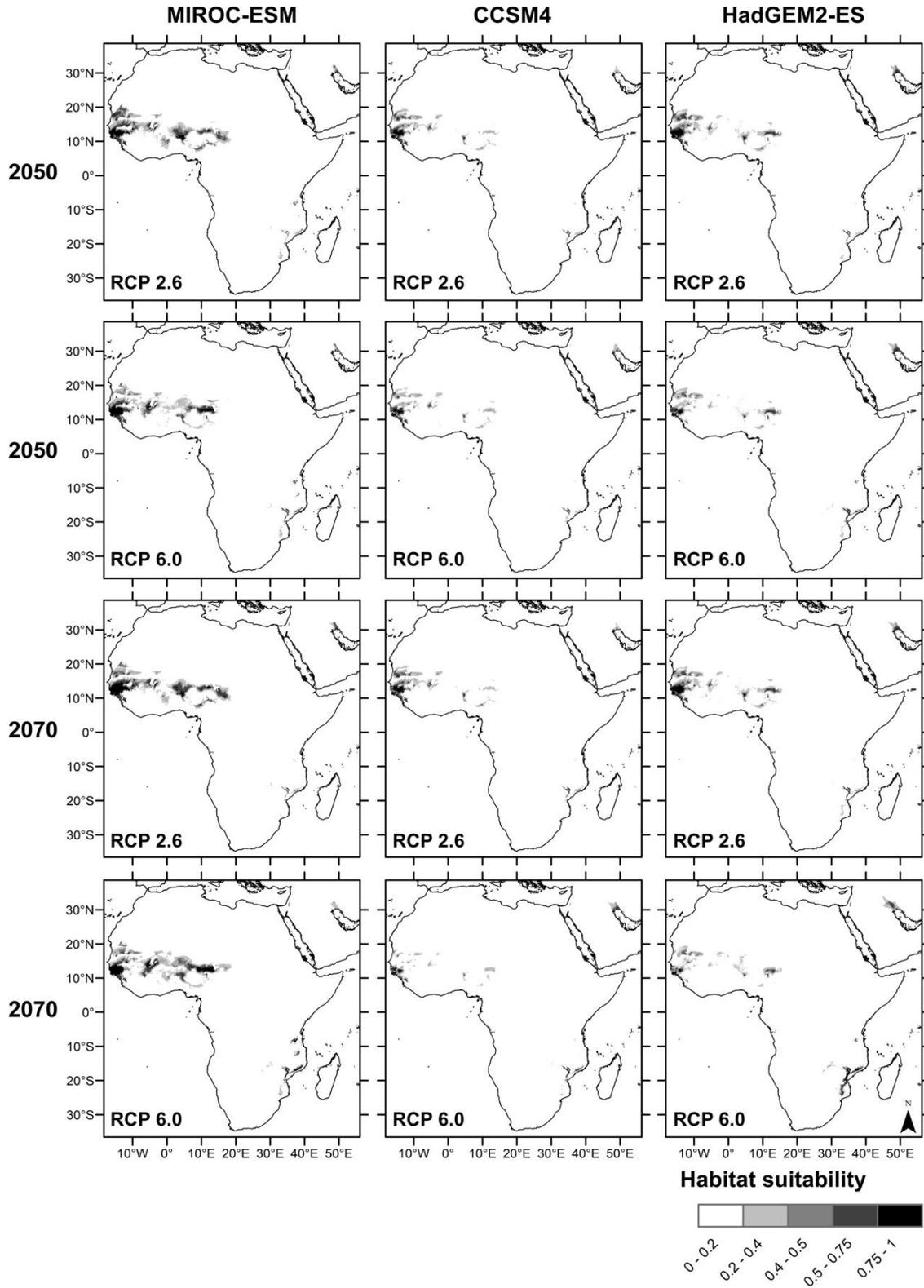
**Figure 1.** Predicted current distributions of the six baboon species: (a) Guinea baboon, (b) olive baboon, (c) hamadryas baboon, (d) yellow baboon, (e) kinda baboon and (f) chacma baboon. Colours indicate habitat suitability: 'ideal' ( $>0.75$ ), 'highly suitable' ( $0.5-0.75$ ), 'suitable' ( $0.4-0.5$ ), 'barely suitable' ( $0.2-0.4$ ) and 'unsuitable' ( $<0.2$ ).



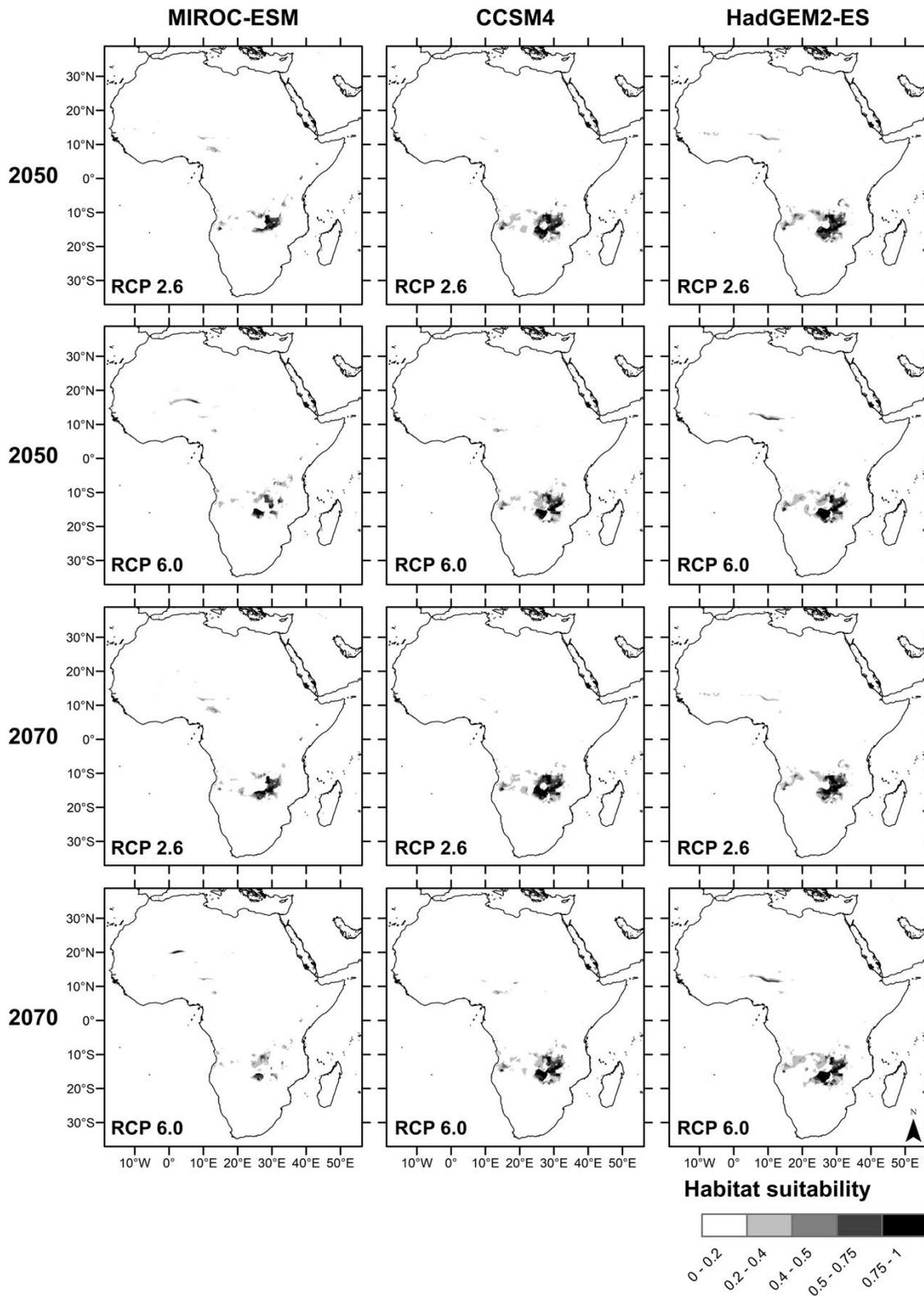
**Figure 3.** Future chacma baboon distribution models across Africa and Arabia according to bioclimatic variables for 2050 and 2070 from three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.6 and RCP6.0). Colours indicate the habitat suitability as ‘ideal’ (>0.75), ‘highly suitable’ (0.5–0.75), ‘suitable’ (0.4–0.5), ‘barely suitable’ (0.2–0.4) and ‘unsuitable’ (<0.2).



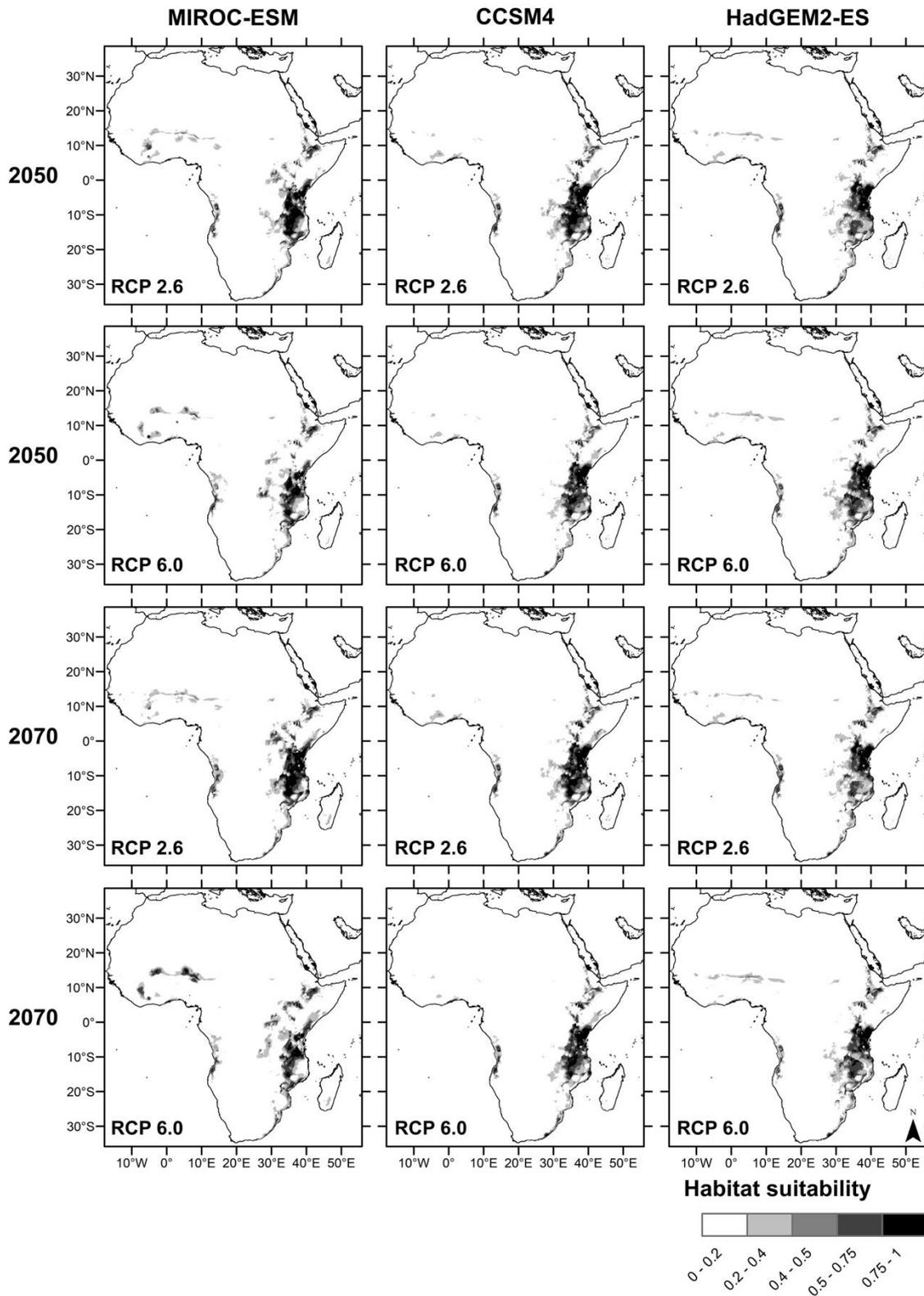
**Figure 4.** Future Guinea baboon distribution models across Africa and Arabia according to bioclimatic variables for 2050 and 2070 from three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.6 and RCP6.0). Colours indicate the habitat suitability as ‘ideal’ (>0.75), ‘highly suitable’ (0.5–0.75), ‘suitable’ (0.4–0.5), ‘barely suitable’ (0.2–0.4) and ‘unsuitable’ (<0.2).



**Figure 5.** Future kinda baboon distribution models across Africa and Arabia according to bioclimatic variables for 2050 and 2070 from three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.6 and RCP6.0). Colours indicate the habitat suitability as ‘ideal’ (>0.75), ‘highly suitable’ (0.5–0.75), ‘suitable’ (0.4–0.5), ‘barely suitable’ (0.2–0.4) and ‘unsuitable’ (<0.2).

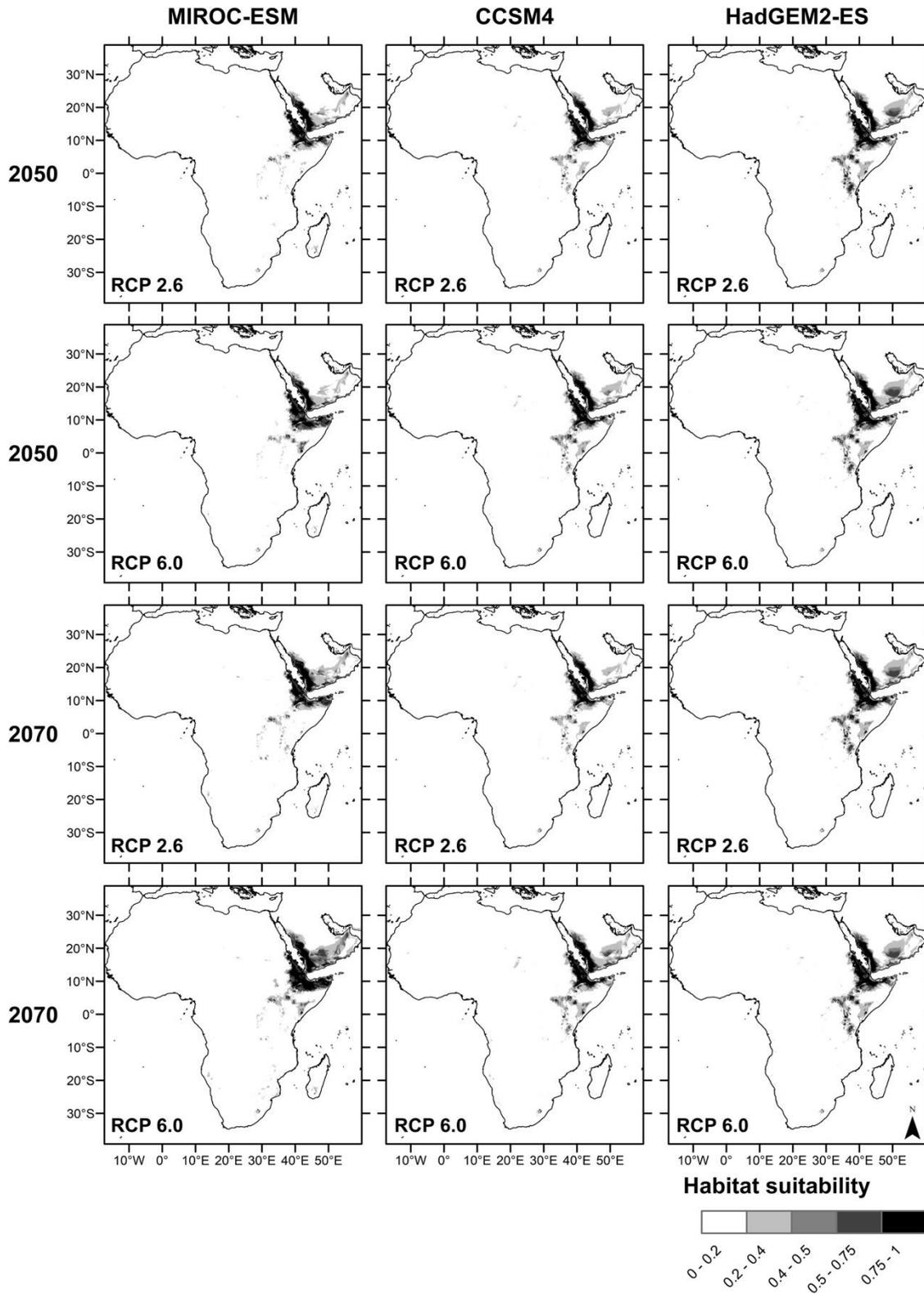


**Figure 6.** Future yellow baboon distribution models across Africa and Arabia according to bioclimatic variables for 2050 and 2070 from three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.6 and RCP6.0). Colours indicate the habitat suitability as ‘ideal’ (>0.75), ‘highly suitable’ (0.5–0.75), ‘suitable’ (0.4–0.5), ‘barely suitable’ (0.2–0.4) and ‘unsuitable’ (<0.2).





**Figure 8.** Future hamadryas baboon distribution models across Africa and Arabia according to bioclimatic variables for 2050 and 2070 from three General Circulation Models (MIROC-ESM, CCSM4 and HadGEM2-ES) under two Representative Concentration Pathways (RCP2.6 and RCP6.0). Colours indicate the habitat suitability as: ‘ideal’ (>0.75), ‘highly suitable’ (0.5–0.75), ‘suitable’ (0.4–0.5), ‘barely suitable’ (0.2–0.4) and ‘unsuitable’ (<0.2).



**Figure 9.** Areas of potential conservation priority for Guinea (a), kinda (b) and chacma baboons (c and d) as predicted from our future distribution models. These are the combined optimal areas (habitat suitability >0.5) under RCP6.0 for models predicting substantial declines in suitable habitat for each species by 2070. The Guinea baboon areas (light grey) combine outputs from the CCSM4 and HadGEM2-ES models, the kinda baboon areas (grey) is based solely on the MIROC-ESM model and the chacma baboon area (dark grey) combines all three models (MIROC-ESM, CCSM4 and HadGEM2-ES).

