

## RESEARCH ARTICLE

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# Ecological niche modeling of the genus *Papio*

Amanda J. Fuchs<sup>1,2</sup> | Christopher C. Gilbert<sup>1,3,4</sup> | Jason M. Kamilar<sup>2,5</sup>

<sup>1</sup>Department of Anthropology, Hunter College of the City University of New York, New York, New York 10065

<sup>2</sup>Department of Anthropology, University of Massachusetts, Amherst, Massachusetts 01003

<sup>3</sup>PhD Program in Anthropology, Graduate Center of the City University of New York, New York, New York 10016

<sup>4</sup>New York Consortium in Evolutionary Primatology, New York, New York 10016

<sup>5</sup>Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, Massachusetts 01003

## Correspondence

Amanda J. Fuchs, Department of Anthropology, University of Massachusetts, Amherst, Massachusetts 01003  
Email: afuchs@umass.edu

## Abstract

**Objective:** Ecological niche modeling (ENM) has been used to assess how abiotic variables influence species distributions and diversity. Baboons are broadly distributed throughout Africa, yet the degree of climatic specialization is largely unexplored for individual taxa. Also, the influence of climate on baboon phylogenetic divergence is unknown. In this study, we constructed ENMs to investigate how niches vary across *Papio* species to understand how climatic variables have influenced their biogeography and mode of speciation.

**Materials and Methods:** We used Maxent to generate ENMs by collating locality data for six *Papio* species and climate information from WorldClim. In addition, we examined the degree of niche overlap among all possible pairs of taxa, which can provide insight into patterns of species diversity. Lastly, we conducted a Mantel test to assess the relationship between niche overlap and estimated time since divergence.

**Results:** Our models performed moderately to extremely well, with a mean area under the curve value of 0.868. The species with the best models include *P. papio* and *P. kindae*, whereas *P. hamadryas* had the poorest models. We found that most species pairs exhibited significantly different niches. Lastly, we found no significant correlation between niche overlap and divergence times.

**Discussion:** Niche models had good predictive power, which indicates *Papio* species distributions are correlated with climatic variables to varying degrees. Significantly little niche overlap and incomplete geographic boundaries suggests these models generally support a parapatric speciation scenario for the genus *Papio*.

## KEYWORDS

Africa, baboons, biogeography, climate, species distribution

## 1 | INTRODUCTION

The ways in which environmental conditions influence the distribution and evolution of species has been a topic of interest for over a century (Darwin, 1859; Grinnell, 1917), particularly in the fields of biogeography, ecology, evolutionary biology and conservation biology. More specifically, the concept of a species “niche” and the ways in which abiotic and biotic variables interact and influence a species’ role and place in an environment may have varying definitions or interpretations (Gaffney, 1975; Hutchinson, 1957; Peterson et al., 2011). Early ecological studies assessed species niches by examining biological patterns and their interactions with geographic and/or environmental variables on a qualitative level, but in the past few decades research has shifted to more quantitative techniques (Elith &

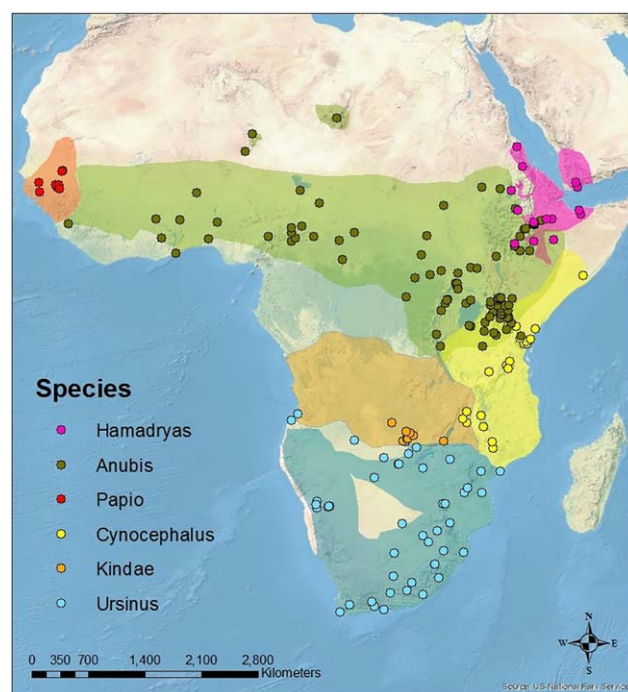
Leathwick, 2009). Scale is also important, both in time and space, when considering factors that influence species ecology and evolution (Elith & Leathwick, 2009; Peterson et al., 2011). By taking a “Grinnellian” approach one may understand the broader impacts of geographic variables on distribution and ecological niches over a larger scale, as opposed to an “Eltonian” approach focusing on local patterns and processes to understand a population’s role and place in an ecological niche (Elton, 1927; Grinnell, 1917; Peterson et al., 2011). Therefore, in recent years, ecological niche modeling (ENM) has become a popular method to assess speciation, ecological diversity, and niche evolution of species on a larger scale, and has recently been used to examine primate distributions and adaptations.

For example, ENM has been used to assess geographical distribution and taxonomic diversity in primate genera, such as *Microcebus* and

*Eulemur* in Madagascar (Blair, Sterling, Dusch, Raxworthy, & Pearson, 2013; Johnson, Delmore, Brown, Wyman, & Louis, 2016; Kamilar & Tecot, 2015; Kamilar, Blanco, & Muldoon, 2016). In the case of *Microcebus*, the models suggested that climatic variables significantly influence the distribution of five out of the six taxa examined. The sixth species, *M. murinus*, had a statistically weaker model, suggesting that this species is likely an ecological generalist less affected by climatic variation. Furthermore, Kamilar et al. (2016) argued that the significantly different niches among *Microcebus* species provide additional evidence that they are separate species. Blair et al.'s (2013) study on *Eulemur* suggested that spatial overlap and incomplete geographic boundaries positively correlate with known hybrid zones, and they accurately depicted niche overlap due to climatic similarity. In addition, one pair-wise comparison found that two different *Eulemur* species resided in notably different environments suggesting that the phylogenetic relationship between these sister taxa was a result of parapatric speciation (Blair et al., 2013). Finally, Blair et al. (2013) further suggested that the remaining comparisons were most consistent with allopatric speciation because there were significant geographic boundaries (i.e., rivers) separating species yet species exhibited similar niches. Ultimately, these studies have shown that constructing ENMs and assessing the degree of niche overlap among species can provide insight to the mechanisms that have influenced speciation in closely related taxa.

The degree to which niches among sister taxa are conserved has also been a topic of debate, and Warren et al. (2008) argue that this may be the result of how niche similarity is measured combined with the null hypotheses being tested. For example, Peterson (1999) found that sister taxa have conserved niches and that speciation takes place as a result of geography, with ecological differences evolving later. In contrast, Graham et al. (2004) suggested that differential selection plays an important role in the separation of closely related species because Dendrobatidae, the family commonly referred to as poison dart frogs, inhabited significantly different niches in Ecuador. These results could be due to different modes of speciation, but Warren et al. (2008) suggest that it may also be a result of various methods whereby Peterson (1999) tested "niche similarity" and Graham et al. (2004) tested "niche equivalency." Thus, Warren et al. (2008) developed consistent methods which include new similarity metrics and randomization tests to quantify the degree of niche overlap among taxa. The new metrics applied by Warren et al. (2008) compare niche models of species pairs and incorporate Schoener's *D* statistic (Schoener, 1968), which has previously been used to assess niche overlap, and Hellinger's *I* statistic, because it has been used to compare community composition across sites.

The genus *Papio* is a widely distributed and intensively studied primate genus, and the speciation patterns that produced the current distribution of baboon species has been a subject of debate (Zinner, Buba, Nash, & Roos, 2011). One way to address questions regarding the complexities of baboon biogeography, evolutionary history and speciation is to construct ENMs. Baboons range throughout most of Africa, even extending into the Arabian Peninsula, and its species inhabit an array of ecosystems including savannas, open woodlands, semi-deserts, and swamps (Figure 1) (Altmann & Altmann, 1973; Kingdon, 2015). The



**FIGURE 1** IUCN range maps and locality data used in this project. *P. anubis*: *N* = 86, *P. cynocephalus*: *N* = 20, *P. hamadryas*: *N* = 17, *P. kindae*: *N* = 9, *P. papio*: *N* = 8, *P. ursinus*: *N* = 46. *N* is the number of localities per species

anubis/olive baboon (*Papio anubis*) has the largest range and inhabits most vegetation types, including the open savannas and woodlands of East Africa and through the central savanna belt toward the rainforests of western Africa, as well as two isolated populations in Chad and Niger (Burrell, 2009; Groves, 2001; Higham, Warren, Adanu, Umaru, Maclarnon, Sommer, & Ross, 2009; Kunz & Linsenmair, 2008; Newman, Jolly, & Rogers, 2004; Winder, 2014). Hamadryas baboons (*Papio hamadryas*) are found throughout the semideserts of Northeast Africa and the Southwestern region of the Arabian Peninsula dominated by semiopen to closed habitats (Groves, 2001; Winder, 2014). Hamadryas are also known to inhabit coastal lowlands of Eritrea (Zinner, Pelaez, & Torkler, 2001). West of the anubis baboons' distribution is the smallest *Papio* species range, Guinea baboons (*Papio papio*), which are found in more forested, coastal environments (Groves, 2001; Zinner et al., 2001). Southeast of the *Papio anubis* distribution is the yellow baboon (*Papio cynocephalus*), ranging through eastern and coastal Africa, from Kenya down to Malawi, dominated by semiopen habitats (Groves, 2001; Winder, 2014). Yellow baboons' range is adjacent to that of the Kinda baboons' (*Papio kindae*) range (Burrell, 2009; Newman et al., 2004), which is dominated by semi-open and closed habitats and includes Zambia, Angola, and southern Democratic Republic of Congo (Groves, 2001; Winder, 2014). Throughout southern Africa, south of the Kinda baboons, are the chacma baboons (*Papio ursinus*), who inhabit semiopen conditions and higher altitudes, such as in the Drakensberg mountains and the areas along the coast surrounding Cape Town, South Africa (Groves, 2001; Henzi, & Barrett, 2003; Hoffman, & O'Riain, 2012). Thus, because of their wide distribution across many

ecotones, abilities to adapt to human modified environments, and broad dietary habits, baboons are often considered ecological generalists.

Five baboon species have been traditionally recognized: hamadryas baboons, anubis baboons, Guinea baboons, yellow baboons, and chacma baboons (Groves, 2001; Hill, 1970). However, in more recent years (and as noted above), morphological and genetic studies have supported the recognition of a sixth species, Kinda baboons (*Papio kindae*) (Groves, 2001; Grubb et al., 2003; Jolly, Burrell, Phillips-Conroy, Bergey, & Rogers, 2010; Szalay, & Delson, 1979; Zinner, Groeneveld, Keller, & Roos, 2009a; Zinner, D., Wertheimer, J., Liedigk, R., Groeneveld, L. F., & Roos, C., 2013). Even though the identification of these six baboon taxa is based on years of research on a variety of biological traits, debate still remains regarding the taxonomic delineation of baboon species. Under a biological species concept (BSC), baboons have been classified as allopatric subspecies of the superspecies *P. hamadryas* (Frost, Marcus, Bookstein, Reddy, & Delson, 2003; Jolly, 1993). This concept may generalize baboon species, excluding hamadryas baboons, under the broad title “savanna” baboons. For instance, Jolly (1993) hypothesized that there was little niche separation between baboons and they should be considered subspecies (however, it should be noted that his views have recently changed regarding species definitions; see Jolly, 2014). Kamilar (2006) examined Jolly’s (1993) hypothesis and determined that baboon species inhabit significantly different environments, but that their ecology follows a latitudinal cline, thus resulting in an inability to falsify that there is little niche separation between baboon species. Frost et al. (2003) also argued for baboons to be considered subspecies because of latitudinal variation in cranial morphology. Alternatively, baboons have also been considered as six separate phylogenetic species by numerous authors, and this seems to be the growing consensus (Groves, 2001; Grubb et al., 2003; Hill, 1970; Jolly, 2007, 2014; Zinner et al., 2009a; Zinner et al., 2013). In this article, we will adopt the phylogenetic species concept (PSC) and refer to the six baboon taxa as separate species.

Complicating matters of species recognition, known hybrid zones exist where baboon ranges overlap. Baboons are morphologically and geographically distinct species, but exhibit no pre- or post-zygotic reproductive isolation (Zinner et al., 2009a). This has led to discordance between mitochondrial DNA (mtDNA) phylogenies on the one hand and morphologically based phylogenies and taxonomies on the other, suggesting that reticulation events and introgressive hybridization has occurred in baboons’ evolutionary history. The conflict between mtDNA phylogeny and morphology is likely, in part, a discordance between mtDNA and nuclear DNA, which results in mitochondrial paraphyly (Zinner et al., 2009a, 2013). Intrageneric hybridization has been reported between anubis and Northern yellow (Alberts & Altmann, 2001; Newman et al., 2004; Tung, Charpentier, Garfield, Altmann, & Alberts, 2008), anubis and hamadryas (Bergman, & Beehner, 2003, 2004; Bergman, Phillips-Conroy, & Jolly, 2008; Shotake, 1981), Kinda and Southern yellow (Burrell, 2009), and Kinda and grayfoot chacma (*Papio ursinus griseipes*) (Jolly et al., 2011). It has also been suggested that hybridization could be occurring between western anubis and Guinea baboons (Zinner et al., 2009a). Intergeneric hybridization

involving *Papio* species has also occurred, though less common, between *Papio hamadryas* and *Theropithecus gelada* (Dunbar & Dunbar, 1974; Jolly et al., 1997) and *Papio* and *Rungwecebus* (Burrell, Jolly, Tosi, & Disotell, 2009; Zinner, Arnold, & Roos, 2009b; Roberts et al., 2009).

Therefore, despite many years of research on the behavior and ecology of baboons throughout Africa, basic questions still remain as to the forces driving the distribution of these taxa and the exact mode of speciation that has occurred or appears to be occurring. This study represents an effort to examine some of these issues through ecological niche modeling and address the following research questions. First, do climatic variables influence the distribution of the living *Papio* species? Second, are baboon species ecological generalists as defined by climatic variation or are they more specialized with distinct climatic niches? Finally, what do the data suggest about the mode of speciation in the genus *Papio*? If climate-based ENM’s have strong predictive power, it would suggest that baboon species distributions are strongly correlated with climatic factors. Conversely, if the models perform poorly, it may indicate that species are ecological generalists and their distributions are not strongly correlated with specific climatic variables. In addition, significant ecological niche overlap between *Papio* species could indicate that allopatric speciation played an important role in modern distribution patterns. In contrast, little niche overlap may be more indicative of a parapatric speciation model.

## 2 | METHODS

### 2.1 | Data collection

Known localities (latitude and longitude coordinates) for each baboon taxon were obtained from published data (Frost et al., 2003; Kamilar, 2006) supplemented with points collected by the first author in Awash National Park, Ethiopia (*P. hamadryas*) and in the Rumphi District of northern Malawi (*P. cynocephalus*). The minimum distance between points was one kilometer. Sample size varied, but ranged from eight to 86 locality points (Table 2). Two of our species, *P. kindae* and *P. papio*, had relatively small samples sizes. These baboon taxa have not been well-studied in the wild and have small geographic ranges, especially *P. papio*. Small samples sizes could produce uncertain models and/or increased type II errors, therefore the results associated with these species should be interpreted with caution.

Current climatic conditions (i.e., bioclimatic variables) were downloaded from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 2.5 arc-minute resolution. We used eight of the 19 climate variables as predictors in the models (Table 1). Variables were selected for several reasons including: (1) they have been applied in previous ENMs of primates with MaxEnt software (three climatic variables: Temperature Seasonality, Minimum Temperature of Coldest Month, Precipitation of Driest Quarter; Blair et al., 2013; Kamilar & Tecot, 2015; Kamilar et al., 2016), (2) they represent seasonal variations in temperature and precipitation, (3) vegetation types are known to respond to variation in these factors and in turn influences baboon feeding ecology (Dunbar, 1992; Henzi, Byrne, & Whiten, 1992; Hill & Dunbar, 2002), (4) baboon physiology and life history are also known to respond to

**TABLE 1** WorldClim bioclimatic variables used in our species distribution models

BioClim 1 = Annual mean temperature
BioClim 4 = Temperature seasonality (standard deviation $\times$ 100)
BioClim 5 = Max temperature of warmest month
BioClim 6 = Min temperature of coldest month
BioClim 12 = Annual precipitation
BioClim 15 = Precipitation seasonality (coefficient of variation)
BioClim 16 = Precipitation of wettest quarter
BioClim 17 = Precipitation of driest quarter

For more detailed descriptions visit <http://www.worldclim.org/bioclim>.

variation in these climatic variables (Beehner, Onderdonk, Alberts, & Altmann, 2006; Gesquiere et al., 2008; Gesquiere, Onyango, Alberts, & Altmann, 2011; Hill et al., 2003). Finally, we note that other nonclimate variables excluded in our models may also influence baboon distributions, but are outside the scope of our current study.

## 2.2 | Data analyses

We used MaxEnt version 3.3.3k (Elith et al., 2011; Phillips, Anderson, & Schapire, 2006; Phillips & Dudik, 2008) to create all species distribution models. We used a four-fold validation approach, which partitions the species occurrence data into four equally sized subsets (Blair et al., 2013; Kamilar & Tecot, 2015). Using this approach is useful because it allows all data to be used for both training and testing the model (Kamilar & Tecot, 2015), which is particularly beneficial with smaller sample sizes, such as the case with *P. kindae* and *P. papio* in our dataset (Blair et al., 2013; Kamilar & Tecot, 2015; Kamilar et al., 2016; Peterson et al., 2011). The success of the models was judged from two criteria, the first being the “area under the curve” (AUC) statistic and the second being the binomial test of omission under a minimum training presence. AUC values assess a given model's ability to predict a species distribution. An AUC value of 1.0 indicates that the model perfectly predicted a given species distribution, and that, therefore, the climatic

variables strongly influence species localities. A value of 0.5 is equivalent to high levels of model uncertainty, with the climate variables having no predictive ability. Following previous studies, models with AUC values ranging from 0.7 to 0.8 were considered moderately good, AUC values ranging from 0.8 to 0.9 were considered strong, and models with AUC values above 0.9 were considered to perform extremely well. Mean AUC values for each species were calculated from the four replicate models (Blair et al., 2013; Elith et al., 2011; Kamilar & Tecot, 2015; Kamilar et al., 2016; Phillips et al., 2006; Phillips & Dudik, 2008; Warren et al., 2008).

Relying solely on AUC values to judge the strength of models can be problematic (Lobo, Jiménez-Valverde, & Real, 2008). Therefore, we also conducted binomial tests of omission under a minimum training threshold to calculate the statistical significance of each model's predictive ability (Blair et al., 2013; Kamilar & Tecot, 2015; Phillips et al., 2006). We considered the binomial test of omission statistically significant if it had a *p* value of 0.05 or lower. This test was performed for each replicate model for each species.

We used the percent contribution value associated with each predictor to assess which climatic variables had the greatest influence on the model. It is important to note that interpreting these results should be done with caution, particularly if variables are correlated, as is typically the case with various measures of temperature and rainfall (Phillips, 2006). In addition, response curves were examined to determine how each predictor was related to the probability of suitable habitat.

The geographical regions for analysis were determined by using range maps from the IUCN combined with the locality data referenced above (Figure 1). Areas that baboons are not known to inhabit (e.g., most of the Congo Basin rainforest) were excluded because including these areas would artificially increase the performance of the models. Furthermore, MaxEnt only requires known locality data to construct species distribution models (Elith et al., 2011; Phillips, Dudik, & Schapire, 2004; Phillips & Dudik, 2008; Phillips et al., 2006). MaxEnt has also been the preferred method for recent primate studies (Blair et al., 2013; Kamilar & Tecot, 2015; Kamilar et al., 2016). Although there are some critics of presence-only modeling approach (Yackulic et al., 2013), MaxEnt has been shown to outperform other distribution modeling methods across varying samples sizes, including models with a small number of localities (Wisz, Hijmans, Li, Peterson, Graham, & Guisan, 2008).

We used ENMTools software (Warren, Glor, & Turelli, 2008; Warren, & Seifert, 2011) to examine the degree of climate niche overlap among baboon taxa. The identity test was performed to assess whether the habitat suitability scores generated from the ecological niche models of two or more species are significantly more different than expected if they were generated from the same distribution. The identity test uses all locality data from both taxa and randomly assigns localities to “pseudo” species pairs. This is done by taking the observed locality points and randomizing the identities to produce a new dataset composed of the same number of localities as the empirical dataset (Warren et al., 2008; Warren, Glor, & Turelli, 2010). There were 99 pseudo species pairs created, and then the real species pair data were compared to this randomized distribution to determine statistical

**TABLE 2** Area under the curve (AUC) values and standard deviation per species, as well as mean AUC across species

Species	Number of localities	AUC (mean)	AUC SD
<i>P. hamadryas</i>	17	0.762	0.060
<i>P. anubis</i>	86	0.795	0.030
<i>P. cynocephalus</i>	20	0.883	0.047
<i>P. ursinus</i>	46	0.882	0.009
<i>P. kindae</i>	9	0.940	0.059
<i>P. papio</i>	8	0.949	0.026
Mean AUC		0.868	



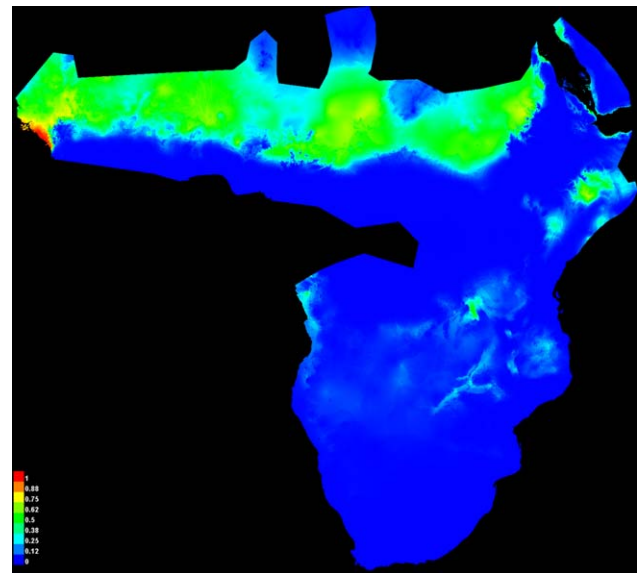
significance (Warren & Seifert, 2011; Warren et al., 2008, 2010). Following the identity test, we used the niche overlap function in ENMtools to measure the similarity between the predicted habitat of each baboon species pair. Niche overlap for pair-wise species comparisons uses Schoener's *D* (Schoener, 1968) and Hellinger's *I* (Warren et al., 2008, 2010) metrics which vary from zero to one. A value of zero indicates no niche overlap between taxa, whereas a value of one indicates complete niche overlap (Warren & Seifert, 2011; Warren et al., 2008, 2010). The 99 pseudo *D* and *I* datasets were generated, and the observed values were then compared to these random distributions to assess statistical significance. A two-tailed test for Hellinger's *I* and Schoener's *D* real values was performed for every species pair comparison to assess the degree of niche overlap. If the observed values fall significantly below the randomly generated values, this suggests no niche overlap between pairs of species. If the observed values fall above randomly generated values, then it would indicate that significant niche overlap exists (Warren et al., 2008, 2010). With a two-tailed test, the two lowest values and the two highest values out of the 99 randomly generated values are considered significant based on an alpha of 0.05.

We also assessed niche breadth by inputting our predicted habitat suitability rasters generated by Maxent for each species (Phillips et al., 2006; Warren et al., 2010). ENMtools calculates niche breadth by estimating the inverse concentration metric developed by Levins (1968). The standardized breadth measurements ranges from zero to one, whereby zero is equivalent to one grid cell being suitable and all other cells are zero, which can be interpreted as a more narrow or specialized niche. A value of one is where all grid cells are equally suitable, suggesting that a species has a wider niche (Nakazato, Warren, & Moyle, 2010; Warren & Seifert, 2011; Warren et al., 2010).

Finally, we examined the relationship between niche overlap and phylogeny using Mantel tests performed in PAST version 3.13 (Hammer, Harper, & Ryan, 2001; Mantel, 1967; Warren et al., 2008). Time since divergence was used as a proxy for phylogenetic distance to determine any correlation between divergence time and the degree of niche overlap among baboon taxa. For the first matrix, we compiled a climate niche dissimilarity matrix based on Hellinger's *I*. The second matrix consists of averages of the estimated divergence dates among all baboon taxa from Zinner et al. (2013). The mtDNA1 data set is the most complete genetic dataset available for baboons, which incorporates as much of their whole genome as possible, thus the divergence dates derived from these data were used as a proxy for phylogenetic distance. In an effort to be conservative and to simplify the complexity of baboon population phylogeny, we selected divergence dates for each species based on the first population to diverge within each species. A second Mantel test was also conducted using Schoener's *D* to quantify niche dissimilarity.

### 3 | RESULTS

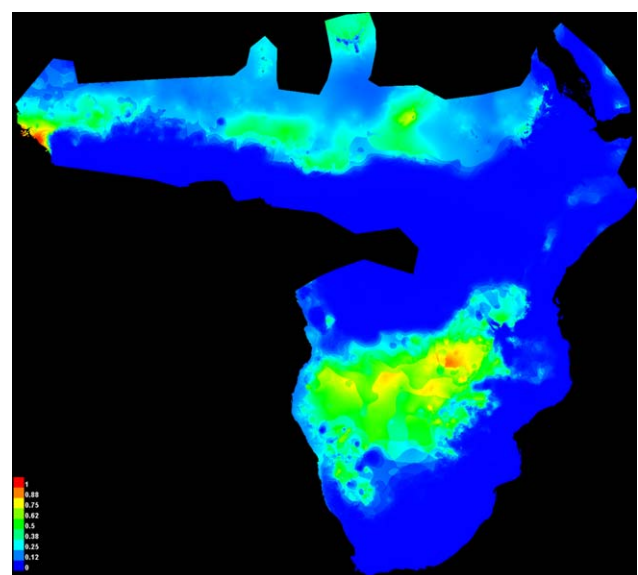
On the basis of AUC values, we found that the climate niche models performed moderately to extremely well for all species. The mean AUC



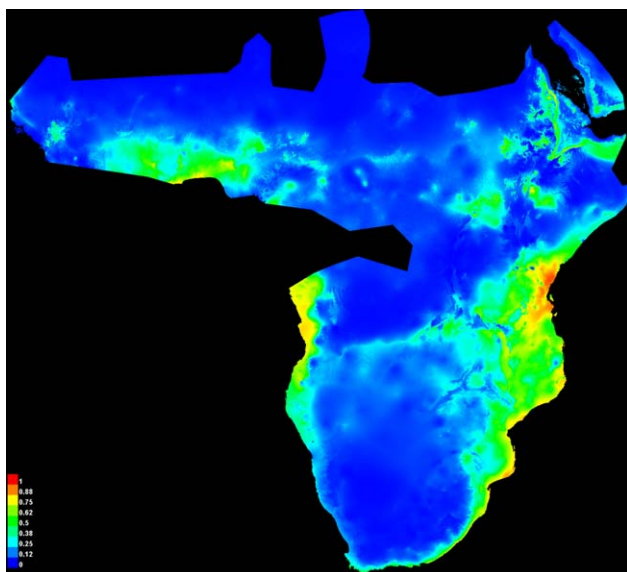
**FIGURE 2** Predicted occurrence map for Guinea baboon (*P. papio*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence

for the six baboon species ENMs ranged from 0.727 (*P. hamadryas*) to 0.949 (*P. papio*), with an average AUC of 0.869 across species (Table 2, Figures 2–7). There was more variation in model performance based on the binomial test of omission results (Table 3). These tests were statistically significant for all four-folds for one species, *P. ursinus*. For two species, *P. papio* and *P. cynocephalus*, three of the four-folds were significant. Also, the *p* value associated with the fourth fold for *P. cynocephalus* was 0.09. One of the four-folds was significant for *P. kindae*, and two others were associated with *p*-values < 0.081. None of the four-folds were significant for *P. hamadryas* or *P. anubis*, though each had one fold associated with a *p* value < 0.10.

F2-F7

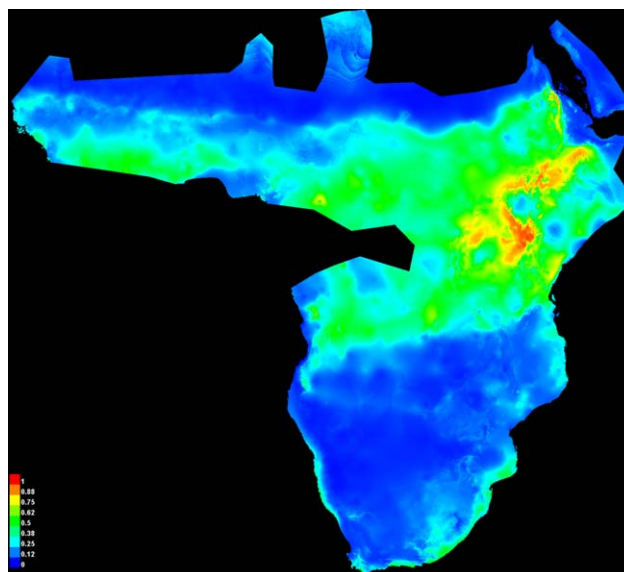


**FIGURE 3** Predicted occurrence map for Kinda baboon (*P. kindae*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence



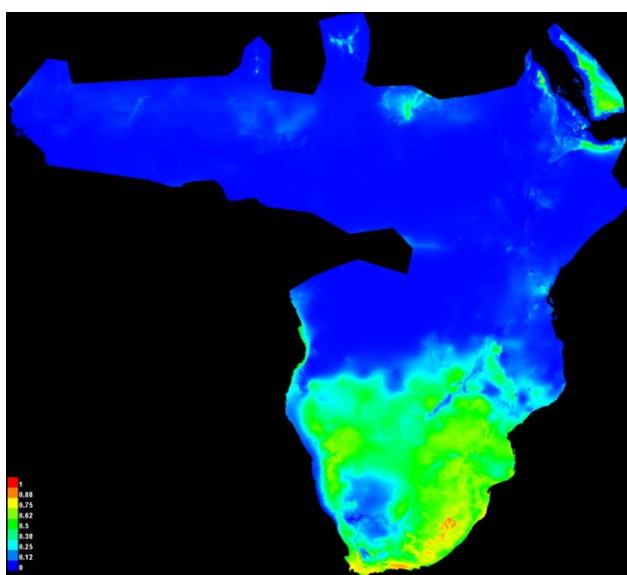
**FIGURE 4** Predicted occurrence map for yellow baboon (*P. cynocephalus*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence

Different climatic variables were more or less important in modeling the distribution of the different *Papio* species as seen with the percent contribution results (Table 4). Based on the percent contribution values, temperature seasonality (BioClim 4) contributed most to the *P. ursinus* (44%) and *P. anubis* (53%) predictive models. Precipitation during the driest quarter (BioClim 17) was the most influential predictor for *P. kindae* (64.5%) and *P. papio* (31.1%). The climatic variable that contributed most to the *P. hamadryas* model was annual precipitation (BioClim 12) at 52%. Lastly, maximum temperature during the warmest month (BioClim 5) contributed the highest percentage to the *P. cynocephalus* with 29.6%.

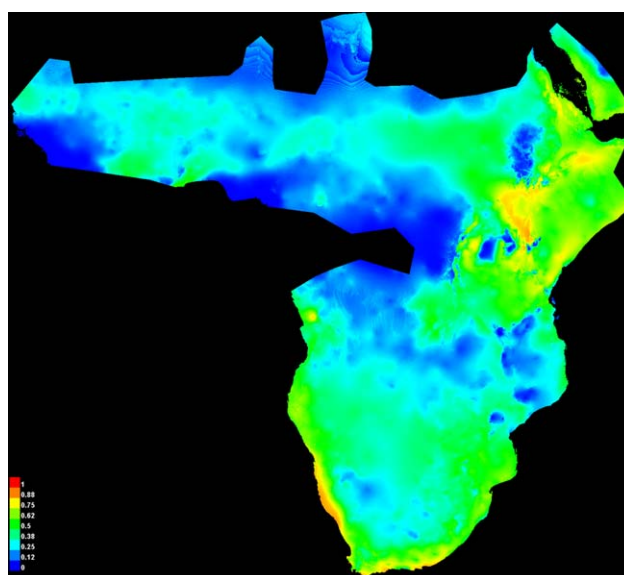


**FIGURE 6** Predicted occurrence map for anubis baboon (*P. anubis*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence

The results of the niche overlap tests indicate that most baboon species exhibit significantly different niches based on Hellinger's *I* and Schoener's *D* (see Tables 5 and 6, respectively). However, for two pairwise comparisons the observed *I*-values fell within the random distribution of values: *P. anubis* vs. *P. hamadryas* and *P. cynocephalus* vs. *P. hamadryas* (Table 5). For Schoener's *D* the same pairs' observed *D* values fell within the random distribution (Table 6). The niche breadth results indicate that some baboon species have narrower niches than others (Table 7). *P. hamadryas* had the highest value, indicating the broadest niche among the species we examined. Three species, *P. kindae*,



**FIGURE 5** Predicted occurrence map for chacma baboon (*P. ursinus*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence



**FIGURE 7** Predicted occurrence map for hamadryas baboon (*P. hamadryas*) based on known localities and climate data. Warmer colors indicated a higher probability of occurrence

TABLE 3 Binomial test of omission based on minimum training presence

Species	Fold_0 rate	p value	Fold_1 rate	p value	Fold_2 rate	p value	Fold_3 rate	p value
<i>P. hamadryas</i>	0.000	0.2436	0.250	0.6779	0.250	0.0775	0.000	0.2886
<i>P. anubis</i>	0.095	0.3059	0.000	0.0885	0.048	0.4225	0.000	0.1563
<i>P. cynocephalus</i>	0.000	0.0103	0.200	0.0185	0.200	0.0303	0.000	0.0919
<i>P. ursinus</i>	0.250	<0.001	0.182	<0.001	0.364	0.0008	0.000	<0.001
<i>P. kindae</i>	0.000	0.0153	0.000	0.0808	0.000	0.0739	0.500	0.1843
<i>P. papio</i>	0.000	0.0039	0.000	0.0069	0.000	0.0078	1.000	1.000

*P. papio*, and *P. ursinus*, exhibited similarly low values, indicating a narrow climatic niche.

In addition, a non-significant relationship between the divergence time among taxa and their niche overlap was obtained. The results of the Mantel test run between Hellinger's *I* observed values and estimated divergence date were not statistically significant (*r* value of 0.236, *p* value of 0.205), as well as for Schoener's *D* (*r* value 0.421, *p* value 0.082). Though, we should note that statistical power for these analyses is very low considering we examined six species.

#### 4 | DISCUSSION

We found that *Papio* species distributions are correlated with climatic variables based on ecological niche models. Seasonal variation in temperature and rainfall best predicted baboon distributions, but the importance of specific climatic variables vary across species. Most species pairs exhibited significantly different niches, thus potentially challenging the common idea that they are ecological generalists, at least in regards to climate. More specifically, species that were once clumped together as "savanna baboons" inhabit very different niches based on climatic variables, and these differences could have implications for interspecific variation in behavior and other aspects of their ecology. In addition, based on our niche breadth results, some species may be more specialized than others. Lastly, there is no significant correlation between the degree of niche overlap and divergence time for *Papio* species, indicating that niche separation is not simply the result of evolutionary time.

Under certain assumptions, our niche models have potential for inferring evolutionary processes and our results indicate that baboons diverged via a parapatric speciation mode. Coyne and Orr (2004) describe parapatric speciation as populations diverging by adapting to local, ecological conditions even while exchanging genes. In this situation, gene flow will be limited, but environmental differences between neighboring populations will be different (Coyne & Orr, 2004). Baboon taxa have adjacent geographic ranges with evidence of gene flow (Zinner et al., 2009a, 2011, 2013) and minimal geographic barriers, though they clearly inhabit different environments based on our models. Therefore, these differential selective environments may have played an important role in their phylogenetic divergence.

The Guinea baboon niche model (Figure 2) showed that precipitation in the driest quarter and high temperatures during the warmest month are key factors influencing their range. It is further supported by Winder's (2014) recent GIS-based analysis of range characteristics which states that Guinea baboons inhabit areas with the highest annual temperature and second highest annual rainfall out of the six widely recognized species. Guinea baboons also inhabit the smallest geographic range and have a low niche breadth value; therefore these variables may be acting as constraints to their distribution. Winder's (2014) results also suggest that Guinea baboons inhabit the narrowest range of conditions compared to other baboon species. It has also been argued that the aridity of the Dahomey Gap (Booth, 1958; Oates, 1988) and/or the degree of specialization (Harcourt & Wood, 2012) may serve as a geographic boundary for the movement of West African primate species. Furthermore, the only *Papio* species to have been

TABLE 4 Percent contribution of predictor variables for each species' distribution model

Species	BioClim1	BioClim4	BioClim5	BioClim6	BioClim12	BioClim15	BioClim16	BioClim17
<i>P. anubis</i>	1	43.6	4.2	4.5	15.4	1.5	10.1	19.8
<i>P. hamadryas</i>	2.5	19.5	2.3	0.2	52	20.6	0	2.9
<i>P. cynocephalus</i>	0.5	27.3	29.6	26.8	7.8	0	0	7.9
<i>P. ursinus</i>	7.8	53.4	26.5	1.1	1.8	0.9	1.6	6.9
<i>P. kindae</i>	0	0.1	0	18.3	0	0	17.1	64.5
<i>P. papio</i>	27.1	0.9	26.1	0	0	0	14.8	31.1

BioClim1 = annual mean temperature, BioClim4 = temperature seasonality, BioClim5 = max temperature of warmest month, BioClim6 = min temperature of coldest month, BioClim12 = annual precipitation, BioClim15 = precipitation seasonality, BioClim16 = precipitation of wettest quarter, BioClim17 = precipitation of driest quarter.

TABLE 5 Summary of niche overlap results based on Hellinger's I

Species	<i>P. anubis</i>	<i>P. cynocephalus</i>	<i>P. papio</i>	<i>P. hamadryas</i>	<i>P. kindae</i>	<i>P. ursinus</i>
<i>P. anubis</i>	1	0.830	0.543	0.895	0.497	0.533
<i>P. cynocephalus</i>	0.04	1	0.473	0.860	0.530	0.679
<i>P. papio</i>	0.01	0.01	1	0.621	0.751	0.331
<i>P. hamadryas</i>	0.28	0.16	0.01	1	0.639	0.761
<i>P. kindae</i>	0.01	0.01	0.01	0.01	1	0.593
<i>P. ursinus</i>	0.01	0.01	0.01	0.01	0.01	1

Above the diagonal are Hellinger's I observed values, below the diagonal are the corresponding *p*-values. Most pair-wise comparisons fell significantly below 99 randomized values, indicating that there is little niche overlap. Two comparisons, both including hamadryas baboons, fell within the range of random values.

reported in the Gap are anubis baboons (Campbell, Teichroeb, & Pateron, 2008). Recent genetic studies using mtDNA have suggested that Guinea baboons are monophyletic, thus their ability to inhabit such unique and specific environmental conditions may be correlated with their divergence from other *Papio* species and more solitary evolution (Zinner et al., 2009a, 2013). However, until nuclear DNA becomes available it is difficult to say for certain what the relationship is between genetics and ecology.

Kinda baboons had the second strongest model based on AUC (Figure 3). Precipitation during the driest quarter was the most important variable. The contributing rainfall and low temperature variables could have implications for Kinda baboon thermoregulation and socioecology. For example, previous studies have shown that primates may be influenced by colder, wetter climates, including elevated thermoregulatory requirements in cold habitats and decreased activity in heavy rainfall (Higham et al., 2009; Hill et al., 2003; Kamilar et al., 2016). The strength of their niche model and minimal niche overlap with other baboons suggest that this species is inhabiting a distinct niche compared to other baboons and further supports its recognition as a sixth baboon species.

The yellow baboon's niche model (Figure 4) also performed well. Based on the model, their most suitable habitats are through Kenya and Tanzania (which in part could be due because of a sampling bias of locality data towards northern sites), but extends south towards Malawi. Yellow baboons were also predicted on the opposite coast in

western Africa, northwest of the Kinda baboons range in Angola, Democratic Republic of Congo, Republic of Congo, and Gabon where there are no known baboon populations. Also, they were not predicted within the Kinda baboons' range which is interesting considering that Kinda baboons were long recognized as a subspecies of yellow baboons. Yellow baboons inhabit lower latitudes with a cooler mean annual temperature compared to hamadryas, anubis, and Guinea baboons (Winder, 2014), which complements our findings.

The variables that contribute most to the chacma baboon niche model indicate that they are better suited for cooler environments and potentially at higher altitudes than other baboons (Figure 5). In fact, previous authors have argued that they have a preference for colder environments (Henzi & Barrett, 2003; Stone, Laffan, Curnoe, Herries, 2013). Interestingly, previous spatial modeling of chacma baboons in southern Africa found that they preferred low altitude with cool temperatures and moderate rainfall, and may only be using the mountains (e.g., Drakensberg) as a result of human modification (Stone, Laffan, Curnoe, Rushworth, Herries, 2012; Stone et al., 2013). However, research on human-baboon conflict in Cape Town found that chacma baboons select human modified environments and resources even when natural resources at higher elevations are available. Thus, this study group has not shifted their range into the mountains to avoid humans (Hoffman & O'Riain, 2013). Therefore, even when human modification is considered, it seems likely that chacma baboons may prefer colder environments to anthropogenic impacts.

TABLE 6 Summary of niche overlap results based on Schoener's D

Species	<i>P. anubis</i>	<i>P. cynocephalus</i>	<i>P. papio</i>	<i>P. hamadryas</i>	<i>P. kindae</i>	<i>P. ursinus</i>
<i>P. anubis</i>	1	0.532	0.287	0.656	0.268	0.211
<i>P. cynocephalus</i>	0.04	1	0.208	0.583	0.278	0.362
<i>P. papio</i>	0.01	0.01	1	0.332	0.446	0.112
<i>P. hamadryas</i>	0.22	0.14	0.01	1	0.400	0.436
<i>P. kindae</i>	0.01	0.01	0.01	0.01	1	0.373
<i>P. ursinus</i>	0.01	0.01	0.01	0.01	0.01	1

Above the diagonal are Schoener's D observed values, below the diagonal are the corresponding *p*-values. Most pair-wise comparisons fell significantly below 99 randomized values, indicating that there is little niche overlap. Two comparisons, both including hamadryas baboons, fell within the range of random values.



**TABLE 7** Standardized niche breadth values generated from ENMtools

Species	Niche breadth
<i>P. hamadryas</i>	0.757
<i>P. anubis</i>	0.618
<i>P. cynocephalus</i>	0.426
<i>P. kindae</i>	0.354
<i>P. papio</i>	0.304
<i>P. ursinus</i>	0.299

Values range from zero to one, with zero being equivalent to one grid cell being suitable and all other cells are zero (specialized niche). A value of one is where all grid cells are equally suitable (broad niche).

Anubis baboons were associated with a moderately performing niche model and a higher niche breadth value (Figure 6, Table 7). This may suggest that they are more ecologically flexible compared to other baboon species (excluding hamadryas who had a slightly lower AUC value and higher niche breadth value). However, the suitable habitat throughout East Africa indicates that this region is the most suitable for anubis baboons, even though locality data from throughout their range was used to construct models. In contrast, there are large areas of high uncertainty throughout central and western Africa that could be a result of this species inhabiting the largest range with the most climatic variability. In general, the areas with low temperature seasonality were found to be their most suitable habitats. Rainfall variables were also important predictors of anubis baboon distributions. Interestingly, existing research on western populations reveals that they inhabit high rainfall areas at a cost. Higham et al. (2009) examined anubis baboons in Gashaka Gumti National Park, Nigeria and argued that rainfall could have significant implications for life history, including longer interbirth intervals and higher infant mortality, as well as decreased foraging time and increased risk for disease. Therefore, they argued that the wild troop at this study site likely represents the extreme rainfall conditions that anubis baboons can tolerate.

Finally, hamadryas baboons were associated with a moderately performing model, which may be due to a variety of factors. For example, the Malagasy primate, *Microcebus murinus*, was associated with a weak model and the authors argued it was a result of this species being an ecological generalist. Therefore, abiotic factors were not exerting strong selective pressures on their geographic distribution (Kamilar et al., 2016). Similarly, the model and niche breadth results could suggest that hamadryas baboons are more ecologically flexible than is generally appreciated. This ecological flexibility could be associated with hamadryas baboons' social system, which is a multilevel society (Abeglen, 1984; Kummer, 1968; Schreier & Swedell, 2009). Studies suggest that this fission-fusion of social groups may be a coping mechanism to deal with food scarcity (Jolly, 1993; Kummer, 1968; Schreier & Swedell, 2012). Thus, this behavioral adaptation to divide into smaller units during times food scarcity may provide this species with the ability to cope with seasonal fluctuations in temperature and precipitation as food availability increases and diminishes. Food availability likely

correlates with annual precipitation, since rainfall is often a proxy for primary productivity and may have implications for baboon ecology (Hill et al., 2003; Deshmukh, 1984; Le Houerou, 1984). Additionally, the niche model predicted hamadryas baboons in Turkana Basin, Kenya, which is near their known range, but currently occupied by anubis baboon. Therefore, one possibility is that competitive exclusion with anubis baboons is playing a role in hamadryas baboons' inability to inhabit this area. Another possibility may be due to their relatively recent divergence time and not having enough time to disperse further than their current range. Lastly, their moderate model performance may be linked to small sample size.

Overall, the niche models performed well, though there are some notable exceptions. For example, Kinda baboons were predicted to partially be in the geographic range of Guinea. This may be due to both species being associated with precipitation during the driest quarter as the most important predictor for their models. Alternatively, Guinea and Kinda baboons have the two smallest sample sizes, a fact that could influence the accuracy of the models. A second notable exception concerns hamadryas baboons, which were predicted into part of the chacma range. This is likely related to both species inhabiting areas with similarly low annual mean rainfall.

The niche overlap tests indicate that baboons exhibit significantly different niches. Little niche overlap with the lack of distinct and prevalent geographic boundaries implies a parapatric speciation mode for the genus *Papio*. Thus, similar to *Eulemur* and *Microcebus* (Blair et al., 2013; Kamilar & Tecot, 2015; Kamilar et al., 2016), environmental determinants such as rainfall and temperature seem to be playing a significant role in *Papio* speciation processes. These results are interesting considering *Papio* is a larger bodied species that may be able to cross geographic boundaries more easily compared to smaller bodied species. Our results do not completely remove the possibility that other evolutionary processes impacted baboon diversity in the past since we are using present distributions to make inferences for historic processes. For example, previous authors have suggested that glacial and interglacial cycles during the Pleistocene left opportunities for periods of isolation and reconnection for baboon populations as savanna biomes expanded and retreated (see Newman et al., 2004; Zinner et al., 2009a, 2011, 2013). However, recent genetic evidence supports a mostly paraphyletic pattern for baboon divergence (Zinner et al., 2009a, 2013).

We note that there were two species pairs whose niches fell within the randomly generated values, indicating that species do not have significantly different niches. Both species pairs included hamadryas baboons. This could be a result of hamadryas' weaker model and over-prediction of their geographic distribution into other species known ranges. However, one of the species pairs was hamadryas vs. anubis baboons. These species form a well-known hybrid zone in Awash National Park, Ethiopia (Bergman & Beehner, 2003, 2004; Bergman et al., 2008; Shotake, 1981). Therefore, the fact that the observed value fell within the randomly predicted values may be associated with the hybridization zone that occurs between these two species. Interestingly, other species pairs that are known to exhibit a hybrid zone showed significantly different niches.

Niche breadth varied across species and supports the idea that better performing models are associated with more specialized, narrower niches, such as Guinea baboons. Alternatively, species with higher niche breadth values are associated with moderately performing niche models (such as anubis baboons), further supporting the notion that this species is more of a generalist. Our results also support the idea that niche breadth is associated with geographic range size. Species inhabiting a smaller geographic range may have lower tolerances to environmental variation compared to species that inhabit larger ranges (Nakazato et al., 2010), and body size may not be the only restriction to range size, but specialization as well (Harcourt, 2000; Harcourt, Coppeto, & Parks, 2005; Harcourt & Wood, 2012).

Lastly, there was a weak positive relationship between time since divergence and the degree of niche overlap, but the results were not statistically significant. It is not surprising that our analysis was not significant because the sample size was very small (six). The moderate positive correlation coefficient and *p* value approaching significance for Schoener's *D* is interesting because it suggests that recently diverged species have more different niches compared to species that diverged in the distant past. However, the fact that there is no significant correlation between the degree of niche overlap and divergence time overall for *Papio* species indicates that niche separation is not simply the result of evolutionary time. In sum, our results further support the idea that ecological variables have had an effect in driving the differentiation of these taxa and fluctuations in climate may have significantly influenced the diversity and complex evolutionary history of *Papio* species.

The radiation of the genus *Papio* throughout Africa is a fairly recent event beginning ~2 Ma (Newman et al., 2004; Zinner et al., 2009a), and both phylogenetic and fossil evidence suggests that this radiation has southern African origins (Gilbert, Steininger, Kibii, & Berger, 2015; Zinner et al., 2009a, 2013). The ability to rapidly disperse and inhabit an array of habitats, and seemingly different niches between species, makes the evolutionary history of *Papio* both interesting and complex. In addition, the importance of climatic variation for influencing biological diversity on a large spatial scale is still open for debate (Dunn, Cardini, & Elton, 2013).

Though it is likely that there will always be debate regarding baboon taxonomy, our results help to shed light on the distribution and delineation of baboon species. The fact that baboon populations inhabit distinct niches with little niche overlap, and that climatic variables are strongly influencing their distribution, suggests that they are more specialized to particular environmental conditions than once was thought. These data combined with behavioral, morphological and phenotypic variability suggests they should be recognized as separate species, as is current practice using the PSC. It seems apparent that environmental variables have long influenced the evolution of baboons. Furthermore, hybridization in combination with the differentiation in niches, minimal niche overlap, and clinal variation in *Papio* biogeography seems to indicate that the speciation process may still be occurring.

Future studies may include building ENMs with reconstructed past climate data and fossil localities to better understand how earlier baboon populations were impacted by the last interglacial (120–140

ka) and last glacial maximum (21 ka). In addition, constructing models with predicted future climate data may provide insight to how global climate change and anthropogenic impacts may influence baboon populations of the future in regards potential shifting ranges and may even aid human-wildlife conflict management. Lastly, ENMs of baboon subspecies may provide insight to how intraspecific climatic variation within a species range may be influencing distribution and delineation within a taxon; whilst also shedding light on earlier speciation processes.

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## ORCID

Amanda J. Fuchs  <http://orcid.org/0000-0003-4557-8263>

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