Assessing Ecological Divergence and Speciation Scenarios of the *Paragalago zanzibaricus* Species Complex Through Climatic Niche Modeling

Evan Miller[1] · Averee Luhrs[1] · Amanda Mancini[2,3] · Mary E. Blair[4] · Luca Pozzi[1]

Abstract

Cryptic species complexes consist of geographically confluent, closely related species that were once classified as a single species. The diversification mechanisms of cryptic species complexes often are mediated by environmental factors, which in some cases lead to ecological speciation. Niche-based distribution modeling can be an important tool in characterizing the extent of ecological divergence between species that may have resulted from environmentally driven speciation scenarios. We used climatic niche modeling to examine the degree of ecological divergence within the *Paragalago zanzibaricus* species complex in East Africa. We expected parapatrically distributed *P. cocos* and *P. zanzibaricus* to display a significant degree of climatic niche distinction and allopatrically distributed *P. zanzibaricus* and *P. granti* to exhibit a degree of niche conservatism. The extent of niche overlap between the three species was assessed by using a Niche Similarity Analysis (NSA) on bioclimatic values. Selected models for all three species exhibited good predictive ability, although the model for *P. cocos* was most optimal and appeared most consistent with its known range. NSA showed that *P. cocos* and *P. zanzibaricus* were statistically more similar than predicted from null distributional values. Results for NSA between the other two species pairings appear to be within the null distribution. The extent of niche overlap between all three species is consistent with the expectations of allopatric speciation processes. Future studies should examine alternative hypotheses for speciation within this group, including the role of sensory drive, interspecific competition, and the impact of Plio-Pleistocene climatic cycles.

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Introduction

Species are arguably the most fundamental taxonomic unit for understanding evolution, behavior, and conservation of life on Earth (De Queiroz, 2007; Mallet, 1995; Mayr, 1963). A major goal in modern evolutionary research is to determine and quantify the patterns and processes that lead to the evolution and diversification of species. The recognition of separate species traditionally involves a concordance of morphological, geographic, and genetic distinction between taxa (Padial et al., 2010). In recent decades, this classification framework has become intertwined with recent technological advances, such as the advent of high-throughput DNA sequencing (Vogler and Monoghan, 2007), growing virtual museum databases (Hawkins et al., 2022; Knapp & Hofreiter, 2010), and the development of geographic information systems (Graham et al., 2004). However, despite recent advancements, both qualitative and quantitative challenges to species recognition remain.

One new challenge to species classification methods is the growing recognition of cryptic species complexes. These complexes involve groups of two or more species that were once classified as a single species due to similar morphological characteristics but were subsequently split based on phylogenetic and other evidence (Bickford et al., 2007; Ceballos & Ehrlich, 2009; Suatoni et al., 2006). Scholars typically argue that cryptic species must be reproductively isolated, exhibit low phenotypic distinction, and be distinguished based on molecular sequence data rather than morphological characters (Jörger & Schrödl, 2013; Zirkle, 1951). However, due to the lack of consensus on species concepts, these metrics should not define cryptic species on their own (Bickford et al., 2007; Mishler & Donoghue, 1982). Furthermore, some scholars have called for a more process-focused comprehensive framework for cryptic species classification that accounts for phenotypic and molecular data in conjunction with gene flow and reproductive isolation levels (Padial et al., 2010; Struck et al., 2018). Evolutionary explanations for the divergence of cryptic species from ancestral populations often is attributed to gradual distinguishment of nonvisual mating cues (Jones & Barlow, 2004; Narins, 1983) or extreme environmental conditions that results in stabilizing selection and reduces morphological change (Schönrogge et al., 2002). In the past two decades, the number of known species of primates has been growing, particularly among lemurs (Mittermeier et al., 2010; Tattersall, 2007), tarsiers (Groves & Shekelle, 2010), and lorisoids (Nekaris & Bearder, 2007). A major reason for this recent taxonomic inflation within primates is putatively due to the increasing recognition of cryptic species complexes within previously nominal taxonomic lineages based on novel molecular data. Despite the extent of the increase of newly recognized cryptic lineages in recent years, biodiversity within morphologically cryptic species is possibly still underestimated, especially within poorly studied taxa (Ceballos & Ehrlich, 2009). As a consequence, even the mechanisms for evolutionary divergence speciation between cryptic species remains poorly understood.

Contrasts of environmental conditions within the range of a species complex can be a powerful driver of evolutionary species divergence. Ecological speciation is the evolutionary process in which reproductive isolation forms between

ancestral populations due to ecologically driven characteristics (Rundle & Nosil, 2005; Schluter & Conte, 2009). Ecological divergence between taxa can occur due to factors that include climate change and/or localized environmental adaptations and reflects phylogenetic distinctions between species (Cab-Sulub & Álvarez-Castañeda, 2021; Cuervo et al., 2021). Thus, quantifying differences in both abiotic and biotic characteristics between taxa can be a useful metric to further quantify the extent of divergence between cryptic species from a species-environment relationship perspective (Kamilar et al., 2016). One potential method to illustrate ecologically driven divergence scenarios within cryptic species complexes involves the use of niche-based species distribution modeling (Franklin, 2010; Peterson, 2011). A niche includes a host of abiotic and biotic conditions that are most consequential to a species' ecological suitability (Hutchinson, 1957; Schoener, 2009). Niche modeling has been shown to be a valuable tool in clarifying environmental factors most consequential for suitability of a species (Pearce & Boyce, 2006; Junker et al., 2012; McDonald et al., 2019) and illuminating potential mechanisms for environmentally driven divergence and speciation (Blair et al., 2013; Broennimann et al., 2012; Hending, 2021; Raxworthy et al., 2007).

The extent of niche divergence over a moderate period of evolutionary time can coincide with modes of speciation (Peterson et al., 1999). In allopatric speciation scenarios, for instance, divergence between lineages is mostly determined by the presence of a prezygotic geographic barrier between populations (e.g., rivers or mountain ranges) that prevents gene flow between them (Barraclough & Vogler, 2000; Coyne & Orr, 2004). These scenarios often result in some degree of niche conservatism, as environmental factors that determine suitability tend to remain more-or-less the same (Wiens & Graham, 2005). Conversely, parapatric or sympatric speciation scenarios tend to involve intrinsic trait-based divergence that leads to reproductive isolation between populations (Coyne & Orr, 2004; Turelli et al., 2001). Thus, parapatric or sympatric speciation scenarios may entail a significant degree of environmentally mediated divergence that leads to ecological distinction between populations and a lack of niche conservatism (Russell et al., 2022; Wiens & Graham, 2005).

The nocturnal primate family Galagidae has exhibited a high proportion of morphologically cryptic species, and the systematics for this group recently underwent numerous changes (Masters et al., 2017; Svensson et al., 2017). Galagid primates exhibit a wide geographic range across sub-Saharan Africa and occupy a host of different bioregions (Nekaris, 2013; Nekaris & Bearder, 2007). Phylogenetic analysis of this clade dates the divergence to the beginning of the Oligocene, ~30 mya (Masters et al., 2017; Pozzi, 2016; Pozzi et al., 2015). Taxonomic revision for this family has historically been common (Butynski et al., 2006), especially as new molecular findings reveal previously unknown and deeply diverged lineages between taxa (Pozzi et al., 2014). One of the most recent changes to the taxonomy of the Galagidae involves the splitting of the former dwarf galago genus *Galagoides* into western dwarf galagos (*Galagoides*) and eastern dwarf galagos (*Paragalago*), as findings indicate a near 20-million-year separation between the two genera (Masters et al., 2017).

The *Paragalago zanzibaricus* species complex consists of three morphologically cryptic eastern dwarf galago species: *P. cocos*, *P. zanzibaricus*, and *P. granti*. *P. cocos* exhibits a geographic range consisting of moist tropical coastal forests in the southeast and lowland riverine forest environments along the Tana River, as well as humid lowland forests at the foothills of the Usumbara Mountains of Tanzania (Butynski & de Jong, 2019; Butynski et al., 2006; Pozzi et al., 2019, 2020). *P. zanzibaricus* is endemic to Tanzania and can be found in lowland moist tropical forest environments north of the Rufiji and Kilombero Rivers from the Udzungwa Mountains in the west to the eastern coast and Zanzibar Island (Butynski et al., 2006; Perkin et al., 2020; Pozzi et al., 2020). *P. granti* exhibits the largest geographic range of the three species, which includes lowland coastal tropical forest and semi-arid woodland in Tanzania south of the Rufiji and Kilombero Rivers and northern Mozambique, and southern Mozambique, Malawi, and northeastern South Africa (Butynski et al., 2006; de Jong et al., 2019; Génin et al., 2016; Pozzi et al., 2020) (Fig. 1). The delineation of *P. zanzibaricus* and *P. granti* is mostly marked by the presence of the Rufiji and Kilombero Rivers; hence, the ranges of the two species can be classified as allopatric. Rivers have been shown to be a major allopatric barrier to geographic distribution for a multitude of other African primate species (Harcourt & Wood, 2012). The distributions for *P. cocos*
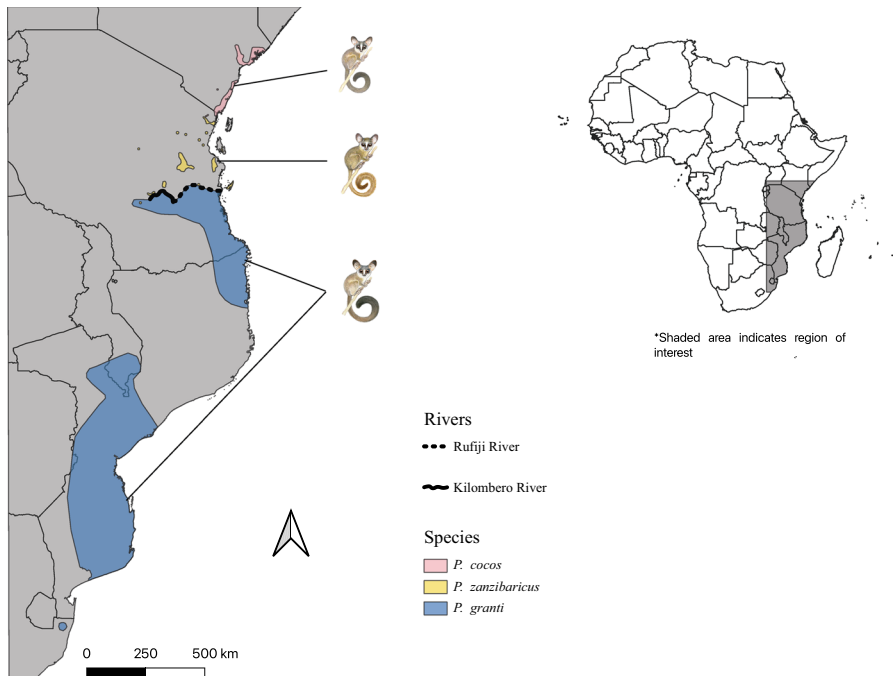

Fig. 1 IUCN range maps of all three species within the *P. zanzibaricus* complex derived from 2019 and 2020 assessments. Illustrations copyright 2020 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission

and *P. zanzibaricus*, on the other hand, appear to exhibit a form of parapatry, because there is no clearly defined geographic barrier between the ranges of these two species.

While the divergence between *P. granti* and the other two species can likely be explained by the presence of the Rufiji and Kilombero Rivers, the speciation scenario for *P. cocos* and *P. zanzibaricus* is less clear. Génin (2021) proposes a *sensory drive hypothesis*. This scenario is based on the recognition concept for species classification, in which a species is regarded as sexually reproducing populations with their own distinct fertilization mechanisms and mate-specific recognition characteristics that are distinguishable from other species (Paterson, 1985, 1993). The sensory drive hypothesis entails that divergence and speciation between populations occur due to environmentally driven changes that affect the composition of mate-specific signals produced, resulting in subsequent reproductive isolation (Cummings & Endler, 2018; Endler & Basolo, 1998). Alternatively, it also has been hypothesized that Plio-Pleistocene global climate change that resulted in widespread contraction of tropical humid forests and expansion of arid grassland and scrub environments could have led to speciation by allopatry, as remaining suitable forest habitat for these species would have persisted on geographically isolated mountain refugia. Parapatry between *P. cocos* and *P. zanzibaricus* may have resulted from secondary contact from forest expansion as the climate warmed (Pozzi, 2016; Pozzi et al., 2019).

In this study, we conducted a climatic niche-based approach to quantify the extent of ecological differentiation that exists between the three species of the *P. zanzibaricus* species complex. We tested the hypothesis that speciation within this complex was at least partially driven by ecological divergence and that the extent of niche differentiation between the three species will be reflective of the given speciation scenario. We expect niche divergence between the three species will reflect allopatric and parapatric speciation scenarios and, moreover, that i) parapatrically distributed *P. cocos* and *P. zanzibaricus* will exhibit a significant degree of niche divergence, and ii) allopatrically distributed *P. zanzibaricus* and *P. granti* will display some form of niche conservatism.

Methods

Climatic Niche Modeling Workflow

All occurrence processing, environmental layer extraction, climatic niche model (CNM) construction, evaluation, projections, and niche similarity analyses were performed on the R-based platform Wallace v.2.0.0 (Kass et al., 2018, 2023).

We first assembled occurrence databases for all three *Paragalago* species. We did not conduct a systematic search, but we integrated an extensive and well documented dataset provided by Butynski et al. (2006) with a couple of more recent studies of the *Paragalago zanzibaricus* complex—Pozzi et al. (2019) and Génin et al. (2016)—that listed localities not included in the original dataset. The final database included presence point data collected from peer-reviewed

publications, in-prep/nonpublished data, and museum label catalogs. Each presence point was georeferenced with a WGS 1984 coordinate reference system and with latitude and longitude coordinates. We then individually assessed each occurrence to determine its accuracy based on the known distributions for each species. The list of all the localities included in the analyses and the sources of these data are available at https://github.com/lucapozzi/paragalago_ENM. We relied on species delimitation data from Pozzi et al. (2020) as well as up-to-date IUCN assessment data for each species (https://www.iucnredlist.org/). To account for potential spatial biases and oversampling in presence point data collection, we spatially thinned remaining occurrences to a radius of 10 km between each locality point. We used the distance of 10 km due to the high spatial heterogeneity of the geographic ranges of these three species, and previous literature indicates that this distance is optimal under heterogenous conditions (Anderson & Raza, 2010; Boria et al., 2014; Pearson et al., 2007). Predictor variables used consisted of all 19 WorldClim bioclimatic variables (bioclims) relating to temperature, precipitation, and seasonality characteristics (Table I) at a resolution of 30 arcsecs (~ 1 km^2 at the equator). We projected occurrence data and raster files in QGIS v3.26 to ensure alignment between raster extents and occurrence points.

Table I All 19 bioclimatic variables (worldclim.org) used as model predictors for the three study species (*Paragalago cocos*, *P. zanzibaricus*, and *P. granti*)

Bioclim variable	Definition
BIO01	Annual mean temperature
BIO02	Mean diurnal range (mean of monthly x (max temp – min temp))
BIO03	Isothermality ((BIO02/BIO07) × 100)
BIO04	Temperature seasonality (standard deviation × 100)
BIO05	Max temperature of warmest month
BIO06	Min temperature of coldest month
BIO07	Temperature annual range (BIO05 – BIO06)
BIO08	Mean temperature of wettest quarter
BIO09	Mean temperature of driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

Model Tuning, Evaluation, and Projection

We selected 10,000 randomly sampled background training points from bioclim rasters for model tuning within selected background extents. The backgrounds we used for both *P. cocos* and *P. zanzibaricus* extended to 1 km around all occurrence points. For *P. granti*, we used a background extent of 3 km around occurrence data due to its expansive geographic range and disjointed distribution. Occurrence data for each species was partitioned into four (k = 4) spatial blocks to independently cross-validate predictive abilities of constructed models. This method of k-fold cross validation involves iteratively withholding one subset (a spatial quadrant block) of occurrences at a time for model testing and evaluation, while the other three are used to train models (Roberts et al., 2017). We trained and tested our models using the maximum entropy (Maxent) modeling algorithm available on Wallace that runs on the maxnet R package. We selected four feature-class combinations (FCs) of models to test that include Linear (L), Linear-Quadratic (LQ), Hinge (H), and Linear-Quadratic-Hinge (LQH). We also applied a range of five regularization multipliers (RMs) to our models adjusted in increments of 1 (1, 2, 3, 4, and 5). The application of RMs to Maxent modeling determines the most causal predictor variables in relation to other variables using an internal variable selection technique called L1 regularization. In typical regression modeling, variables are removed at some correlation threshold to reduce multicollinearity (Symonds & Moussalli, 2011). However, the L1 regularization algorithm used in Maxent modeling shrinks (penalizes) variable coefficients with each RM iteration until some become zero and are not used in the final model (Elith et al., 2011; Merow et al., 2013). This means that even highly correlated variables can be included in model training, because Maxent discards redundant information to gain novel information even when it is relatively small.

Selection of optimal CNMs for each species involved both threshold-dependent and threshold-independent metrics to balance predictive performance against being overfit. The first threshold-dependent metric we prioritized in model selection involved sorting out models with the lowest average omission rate (OR) of presence points. The two average OR metrics available to assess on Wallace include OR at the minimum training presence threshold (OR.MTP) and OR at the 10% training presence threshold (OR.P10). The latter is derived from omitting 10% of calibration records that have the least suitability scores (Mothes et al., 2020). For this initial step, we opted to scrutinize models that exhibited the lowest OR.P10 value rather than the lowest OR.MTP value, as it is generally stricter threshold and omits occurrence points that are likely less representative of true niche suitability. The next step was to pool all models that exhibited an OR < 10%. Once models were pooled, we selected a subset of models out of this pool based on their optimal threshold independent Receiver Operating Curve or Area Under the Curve (AUC) metrics. We interpreted optimal AUC values for model prediction to be ≥ 0.85, although any models with AUC scores higher than 0.50 were still considered to be good. Of the models that had the most optimized OR and AUC values, we then selected models that exhibited the lowest Corrected Akaike Information Criteria (AICc) score relative to other models in this pool. AICc scores can be considered an

important metric in niche model evaluation, as it is indicative of model complexity in terms of the number of variables used to explain resultant models (Sillero et al., 2021).

Predictive suitability for each species using CNMs of best fit were then projected on a continuous cloglog scale using a polygon of East Africa formatted in QGIS v3.26. In addition, we calculated minimum training presence (MTP) and tenth percentile training presence (P10) thresholds on Wallace. The MTP threshold ascertains the lowest predictive suitability value for a niche model and assumes that this suitability value is the minimum for which this species occurs. In contrast, the P10 threshold, assumes that 10% of occurrences used in model construction found in the least suitable habitats are not representative of the species' overall habitat suitability characteristics, and thus, omits a greater area than the MTP threshold (Pearson et al., 2007). We calculated the area of suitability (in km^2) for both thresholds and for all species by plotting projections of MTP and P10 suitability as GeoTIFF raster files from Wallace into QGIS v3.26 and summing up the total areas of occupancy for all three species. Bioclimatic variables that had the most explanatory power over selected CNMs are included as coefficients in the final optimally tuned models (lambda values (λ)) and were reported for all species.

Environmental Space Analysis

Environmental space analyses on Wallace v2.0.0 rely on statistical comparisons between background bioclimatic rasters within geographic extents of each species and are independent of generated CNMs. We conducted a series of Schoener's D Niche Similarity Analyses (NSA). This type of analysis evaluates the extent to which an environmental niche in one range is more or less similar to an environmental niche in another range than expected by chance. Null distributions are obtained by randomly shifting the density of occurrences in one range of a species and comparing this simulated environmental niche to the observed niche in the range of the other species (Broennimann et al., 2012). If the observed overlap between assessed ranges is greater than 95% of simulated test values, then niches are more similar to each other than expected. Alternatively, if the observed overlap is less than 95% of simulated values, then the niches are less similar to each other than expected (Broennimann et al., 2012; Warren et al., 2008). The metric used to assess the extent of overlap in this test is Schoener's *D*, which ranges from 0 (no overlap) to 1 (100% overlap) (Schoener, 1968; Warren et al., 2008; Broennimann et al., 2012). We generated 100 null values for each species pairing and tested overlap using a two-sided D-test at an alpha level of 0.05 assuming that niches could be less similar than expected (lower 5th percentile) or more similar than expected (higher 5th percentile) based on null parameters.

Ethical Note

Our study relied exclusively on digital occurrence records collected from georeferenced museum specimens, publications, and unpublished observation data. We did not employ any methods that would have caused harm or suffering to live wild or captive animals of the three species in the *P. zanzibaricus* complex.

Data Availability All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data and codes related to this paper may be requested from the authors or retrieved from https:// github.com/lucapozzi/paragalago_ENM.

Conflict of Interest The authors declare no conflict of interest.

Results

Climatic Niche Model Selection and Characteristics

Sample sizes of occurrences used for each species varied due to both occurrence data availability and application of spatial thinning and processing techniques. *P. cocos* had the lowest processed occurrence sample size, whereas *P. zanzibaricus* and *P. granti* had similar sample sizes (Table II). Selected models for each species also differ in terms of both feature class and regularization multiplier (Table II). Omission rates for selected models of all three species are optimal ($<10\%$), as was the predictive ability of the model for *P. cocos* as assessed by the AUC metric (0.895; Table II). The selected model for *P. zanzibaricus* and *P. granti* exhibited, although not as optimal, exhibit good predictive scores (0.790 for *P. zanzibaricus* and 0.801 for *P. granti*), even though the AUC metrics for these two models were the highest of their candidate model pools (Table II). Delta AICc criteria in selected models also are not optimal, but this is because omission rate and average AUC metrics were given priority in selection standards.

Model Geographic Projection and Climatic Sensitivity

Model projections of CNMs yielded similar geographic climate suitability between *P. zanzibaricus* and *P. granti* (Fig. 2). However, the projected model for *P. zanzibaricus* indicates that climatic niche suitability was high throughout southern Tanzania and Mozambique (Fig. 2). This geographic area is substantially more extensive than the accepted distribution for this species as postulated by Butynski et al.

Table II Summary of characteristics and metrics for selected candidate climatic niche models (CNMs) for the *Paragalago zanzibaricus* species complex

Species	N	FC	RM	AUC	OR.P10	AICc	deltaAICc	ncoef
Paragalago cocos	24	LQH	2	0.895	0.0833	527.30	3.96	8
Paragalago zanzibaricus	38	LQH	5	0.790	0.0555	852.89	8.95	4
Paragalago granti	36	LQ	3	0.801	0.0750	1073.03	5.63	7

[*]N = occurrence sample size; FC = feature class; RM = regularization multiplier; AUC = Receiver Operating Curve for model test values; OR.P10 = omission rate for 10th percentile training presence threshold; AICc = Akaike Information Criteria (corrected for low sample sizes); deltaAICc = AIC correction value; ncoef = number of model parameters (coefficients)

(2006) (Fig. 2). The model projection for *P. granti* indicates areas of high climatic suitability north of the Rufiji River in Tanzania, contrasting from the accepted distribution for this species (Fig. 2). *P. cocos* exhibited the most restricted range of climatic niche suitability based on CNM projections, with most of its high suitability occurring along the coast of eastern Kenya and a small region in northeastern Tanzania (Fig. 2). Of the CNM model projections for each of the three species, the climatic niche suitability range for *P. cocos* is the most consistent with its known and accepted geographic distribution (Fig. 2). Both P10 and MTP threshold-derived suitability areas for *P. cocos* are significantly smaller than the metrics for *P. zanzibaricus* and *P.granti* (Table III). The areas of suitability assessed by both thresholds are highest for *P. granti*, ranging from ~1.1 to 1.5 million km^2 respectively (Table III). The model for *P. zanzibaricus* also displayed a degree of high climatic niche suitability in coastal Kenya and Tanzania, despite the contrast with its known distribution (Fig. 2). The predictor variable in selected models show that all three species exhibited some degree of sensitivity to *Precipitation of The Coldest Quarter* (BIO19) (Table IV). In addition, selected models for *P. cocos* and *P. granti* suggest heightened sensitivity to *Mean Diurnal Range* (BIO02) (Table IV). Models for *P. cocos* and *P. zanzibaricus* indicate an overlap in positive responses to *Annual Precipitation* (BIO12) and positive responses in the hinge feature class for *Precipitation of The Driest Quarter* (BIO17) (Table IV).

Environmental Space Analysis

NSA as assessed by the two-tailed Schoener's D-test indicate that the niches occupied by *P. cocos* and *P. zanzibaricus* in terms of background extents are significantly more similar to each other than to be expected (D = 0.48, *P* = 0.03; Fig. 3). The
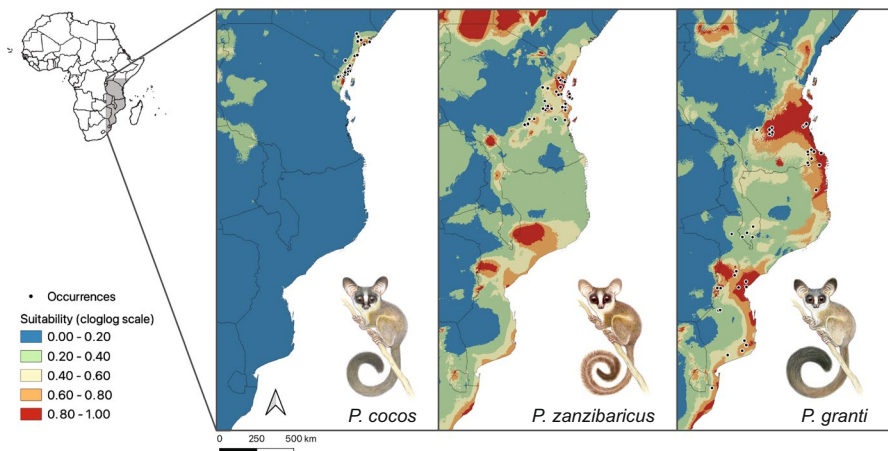

Fig. 2 Climatic niche model suitabilities of optimally tuned models projected as a cloglog scale over an MCP of East Africa for *Paragalago cocos* (left), *P. zanzibaricus* (middle), and *P. granti* (right). 0.00 = least suitable; 1.00 = most suitable. Illustrations copyright 2020 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission

Table III Minimum training presence (MTP) and 10th percentile training presence (P10) threshold values and areas of suitability (reported as 3 significant figures) derived from selected CNMs of the *P. zanzibaricus* species complex. Areas of suitability calculated for these threshold values assume binary occupancy values (1 s vs. 0 s, or presence vs. absence), and the areas estimated encompass all known locations with predicted presences (1 s)

Species	Threshold value		Suitability area (km^2)	
	MTP	P10	MTP	P10
Paragalago cocos	0.136	0.291	3.17×10^5	7.30×10^4
Paragalago zanzibaricus	0.312	0.441	9.53×10^5	5.76×10^5
Paragalago granti	0.212	0.302	1.54×10^6	1.11×10^6

Table IV Bioclimatic sensitivities summarized in terms of Maxent lambda (λ) values multiplied by a factor of 1,000 for each of the three species analyzed in the study (*Paragalago cocos*, *P. zanzibaricus*, and *P. granti*). Maxent lambda (λ) values describe the weights of each predictor variable in the final optimally tuned models

Predictor variables	*Paragalago cocos* λ	*Paragalago zanzibaricus* λ	*Paragalago granti* λ
BIO02	I(-0.0713)^2	0	-22.5
BIO03	0	0	0
BIO06	0	0	6.04
BIO08	0	0	I(0.0156)^2
BIO09	I(0.00607)^2, Hinge(651)	0	0
BIO12	Hinge(1100, 2190)	1.51	0
BIO14	0	23.1	85.4
BIO15	0	0	I(-0.0309)^2
BIO17	Hinge(867)	Hinge(660)	0
BIO18	-9.78	0	3.55
BIO19	1.83	Hinge(403)	I(-0.139)^2

[*]Denotation of λ values derived from Maxent lambda format. λ = raw value; Hinge(λ) = hinge feature class; I(λ)^2 = quadratic feature class

pairings for *P. zanzibaricus* and *P. granti*, as well as *P. cocos* and *P. granti* appear to be within null distribution (for *P. cocos* and *P. granti*: D = 0.02, P = 0.36; for *P. zanzibaricus* and *P. granti*: D = 0.67, P = 0.35).

Discussion

In this study, we assessed the extent to which niche divergence has occurred between all three species in the *P. zanzibaricus* complex under parapatric and allopatric speciation scenarios. Selected models for only *P. cocos* exhibited optimal predictive ability. However, models for the other two species still explained > 50% of suitability and, therefore, can still be considered modestly predictive. The CNM selected for *P. cocos*
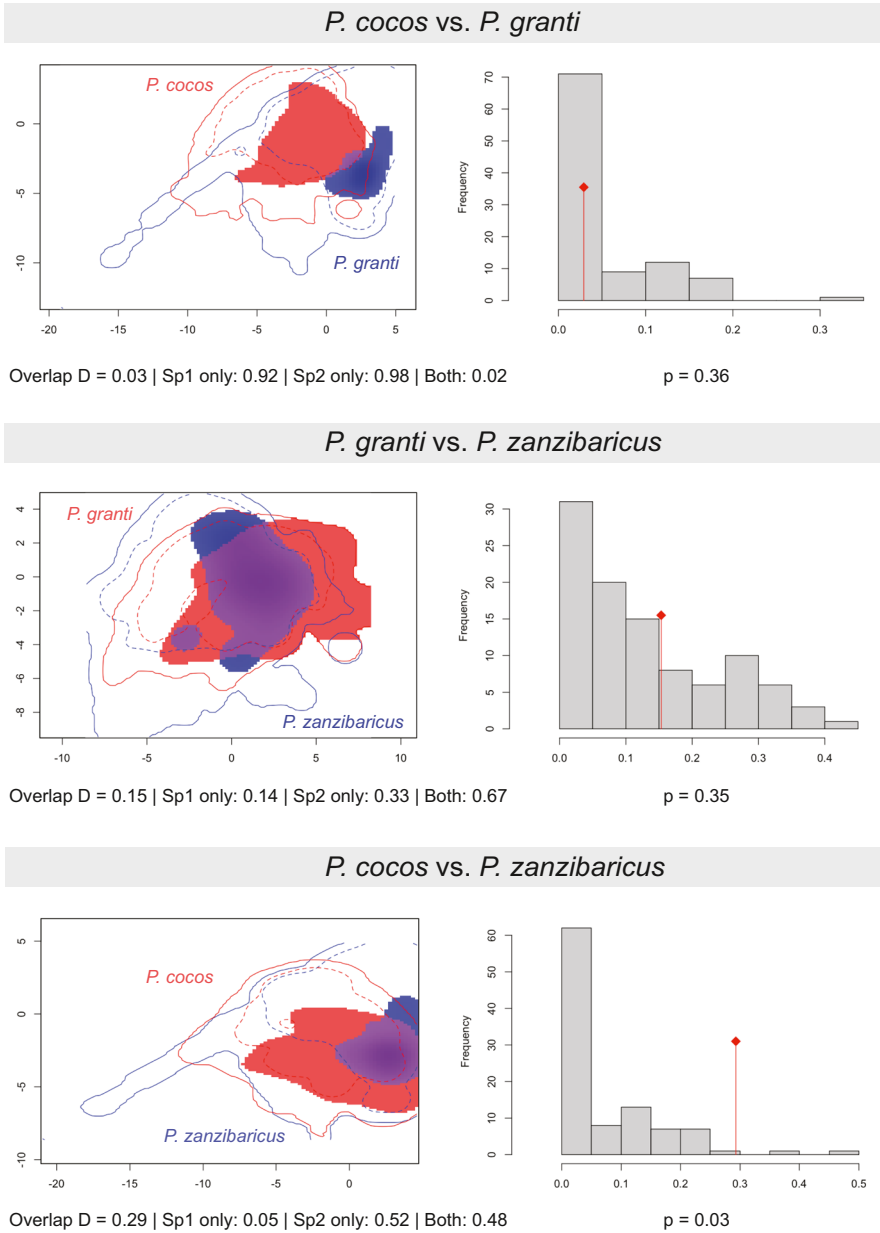
Fig. 3 Environmental space overlap (left) and Schoener's D niche similarity test results (right) between pairings of all three species (*Paragalago cocos, P. zanzibaricus,* and *P. granti)*

indicates that areas of highest suitability only occur in an area surrounding the species' known geographic range. Models for *P. zanzibaricus* and *P. granti* indicate large areas of high suitability well outside of their ranges. However, overprediction is common

for CNMs, because this type of modeling does not take into consideration nonclimatic factors limiting species distribution, such as competitor species and geographic barriers (Iverson et al., 2008; Lawler et al., 2006; Zhang et al., 2015). One factor that could potentially explain lower AUC metrics for these two models is that the background extents used to tune models were not large enough. The AUC value of models has been criticized as a metric, because it has been found to be highly influenced by the size of geographic extent (Lobo et al., 2008). A study area needs to have a large enough proportion of environmentally distinct unoccupied habitats for a model to be able to discriminate more accurately the suitable from unsuitable habitat areas (Phillips et al., 2006; Smith, 2013). Thus, high model predictive performance for *P. cocos* can likely be at least partly explained by the large proportion of deeply unsuitable habitat throughout the region of East Africa outside most of its known range. Additionally, it is reasonable to suggest that *P. zanzibaricus* and *P. granti* are climatic generalists and that climate is likely not the only predictor of ecological suitability. For instance, elevational data on occurrences for *P. granti* in our dataset mostly ranges from 80–500 m above sea level. However, there were five occurrence points from our model dataset that were collected from 1,000–1,550 m above sea level. There have been some records of this species being found up to 1,800 m (de Jong et al., 2019).

In addition to the wide extent of climatic heterogeneity within occurrence data for *P. granti*, taxonomic uncertainties could be responsible for low model predictability in our models. The distributional information currently available for *P. granti* shows a disjoint distribution: northern populations occur from the Kilombero-Rufiji River and Udzungwa Mountains of southeastern Tanzania, southwards through the northeastern coastal region of Mozambique, whereas the southern populations occur in southern Malawi, central and southern Mozambique, south to Tshanini Nature Reserve in extreme northeastern South Africa (Génin et al., 2016; de Jong et al., 2019). The primary causes of this disjoint distribution are currently unknown. It is possible that the historical lack of research in northern Mozambique contributed to our understanding of the true extent of distribution of *P. granti*. Indeed, the range of this taxon was recently extended into South Africa after field observations in the sand forest of Tembe Elephant Park and the Tshanini Community Reserve, near the Mozambique border (Génin et al., 2016). According to the authors, this species was likely formerly mistaken for *Galago moholi.* Alternatively, it is possible that the majority of northern Mozambique is not suitable for this species, as also indicated by our CNM projections (Fig. 3), raising interesting questions about the biogeography and taxonomy of this taxon. Taxonomic classifications have suggested that the population found in montane environments of southern Malawi should be considered a distinct species known as the Malawi dwarf galago (*P. nyasae;* Grubb et al. 2003, Pozzi et al., 2014). Interestingly, our study indicates relatively low ecological suitability for *P. granti* in Southern Malawi, the area where *P. nyasae* was originally described. Unfortunately, limited research has been conducted on this putative taxon and it should currently be considered a synonym of *P. granti* (de Jong et al., 2019). Future studies should be investigate the genetic diversity along the distributional range of *P. granti* to elucidate intraspecies variation, including the relationships between the southern and northern populations, and the taxonomic status of populations in southern Malawi.

Model occurrence data for *P. zanzibaricus* mostly ranged between 50 and 400 m above sea level, but there were four occurrences in the dataset that ranged between 1,200 and 2,450 m above sea level. *P. zanzibaricus* has been shown to select for predominantly secondary lowland forest environments (Honess et al., 2013). However, in the Udzungwa Mountains and other forests of the Eastern Arc Kountains, this species follows up strands of riverine forests up to 1,200 m asl. It is unclear at this time whether those high-altitude presence points for *P. zanzibaricus* are representative of their true geographic range or if the species represented in our data are possibly being confused with other species in the *Paragalago* genus. More validation is needed for high-altitude occurrences of this taxon collected at submontane and montane forest environments of the Uluguru, Udzungwa, and Usambara mountain ranges, because at least some could be mistaken for the sympatric mountain dwarf galago (*P. orinus*) (Perkin, 2001, 2021). The ranges of both *P. zanzibaricus* and *P. granti* also are partially sympatric with the known range of *P. rondoensis* (Honess et al., 2008).

Precipitation variables appeared to have the most impact on suitability for all three species. Models for *P. zanzibaricus* and *P. cocos* suggest that these two species respond particularly positively to precipitation, notably *Annual Precipitation* (BIO12) and *Precipitation of The Driest Quarter* (BIO17). Given their high degree of specialization in wet and humid coastal forest environments of eastern Kenya and Tanzania, it is reasonable to infer that greater precipitation experienced in these environments may lead to improved habitat quality and higher food abundance (Perkin, 2001; Butynski et al., 2006; Butynski & Jong, 2019; Perkin et al., 2020). Because BIO12 indicates drought incidence (Blair et al., 2013), higher levels of precipitation in their environments during drier months may especially augment suitability for these two species by prolonging food and cover availability for longer periods of the year. This also could explain positive responses in the models for both species exhibit to *Precipitation of The Coldest Quarter* (BIO19). The model selected for *P. granti* exhibits a notably positive response to the variable for *Precipitation of The Driest Month* (BIO14), as well as a substantially negative response to the variable for *Isothermality* (BIO02). The geographic range of this species consists of cooler, drier, and more more seasonal scrub-forest environments that are at much higher latitudes than the ranges of *P. cocos* and *P. zanzibaricus* (Génin et al., 2016; de Jong et al., 2019). It is reasonable to infer that higher levels of precipitation during drier months of the year throughout *P. granti*'s range could contribute to a greater abundance of food resources during times when these resources are otherwise scarcer. Similarly, greater fluctuations in temperature throughout the year also could potentially yield greater fluctuations in available food resources for *P. granti*, which may explain this species' negative response to BIO02. Interestingly, one of the morphological differences between *P. cocos* and *P. granti* is the length of the external ear that could be possibly connected to an adaptation in living in different environments: longer ears are more common in dry, open habits, whereas shorter ears are more likely to be found in dense, humid forests (Génin, 2021).

Niche divergence has been demonstrated in the past to be a powerful metric for evaluating species diversification, because it typically entails isolated populations

adapting to new environmental conditions across a landscape that leads to reproductive isolation and subsequent speciation (Nosil, 2012; Pyron & Burbrink, 2009). The degree to which niches are conserved or diverge between shared ancestors of a species is constrained largely by the ability of populations to respond and adapt to climatic and environmental conditions (Futuyma, 2010; Wellenreuther et al., 2012). Ecological speciation, particularly under parapatric distribution conditions, also is restricted by the extent of genetic diversity and the size of effective population sizes found in populations that occur in marginal areas of a species' geographic range, as well as the evenness of gene flow between these marginal populations and central populations within the range (Bridle & Vines, 2007; Kirkpatrick & Barton, 1997).

We hypothesized that niche divergence would be highest with parapatry and that niche conservatism would be highest for allopatry. The results for our niche similarity analyses appear to be consistent with allopatric speciation expectations for all three species. Moreover, climatic niches occupied by parapatrically separated *P. cocos* and *P. zanzibaricus* are statistically more similar to each other than expected by null distribution, rejecting our hypothesis for niche divergence under parapatric speciation expectations. The lack of niche separation between *P. granti* and the other two species of this complex can likely be explained by the presence of the Rufiji and Kilombero Rivers that delineate its northernmost range from *P. zanzibaricus*. These two rivers are the most plausible geographic barriers that drove allopatric speciation between *P. granti* and *P. zanzibaricus*. In terms of high niche similarity between *P. cocos* and *P. zanzibaricus*, the most plausible explanation for speciation between them under an allopatric scenario is that divergence was driven by forest contraction during Plio-Pleistocene climatic fluctuations (Pozzi, 2016). During dry periods, forested habitats retreated to higher elevation in the Eastern Arc Mountains, leaving more arid habitats at lower altitude (Bobe, 2006; deMenocal, 2004). Forest dwelling species, such as the dwarf galagos, might have undergone allopatric speciation while isolated in fragmented forests. Phylogenetic studies conducted on the *P. zanzibaricus* complex have dated the split between *P. zanzibaricus* and *P. cocos* to approximately 3 million years ago, close to the start of the Plio-Pleistocene (Pozzi, 2016; Pozzi et al., 2019, 2020). The current parapatric distribution between *P. cocos* and *P. zanzibaricus* could be potentially explained by secondary contact that resulted when humid tropical forest environments re-expanded millions of years later. Similar phylogeographic patterns have been identified in other taxa indigenous to montane forest environments, including shrews (Stanley & Olson, 2005), amphibians (Lawson, 2010), and birds (Bowie et al., 2006).

While it can be inferred that allopatric speciation expectations are upheld for this species complex, there is a multitude of cases in which divergence and speciation cannot be explained by intraspecific or interspecific niche differentiation (Rundle & Nosil, 2005; Schluter, 2009; Sobel et al., 2010). For example, ecological niche radiation likely did not play a significant role in the divergence of several odonate insects (dragonflies and damselflies) and that speciation was more likely driven by factors, such as sexual selection and other social cues (McPeek & Gavrilets, 2006; Svensson et al., 2004). High niche overlap in a parapatric distribution setting also can sometimes be explained by high, interspecific competition, in which two or more species occupy similar climatic niches and tolerate similar abiotic/biotic conditions but cannot

coexist as a result of competitive exclusion (Jezkova & Wiens, 2018; Russell et al., 2022). Competition has been demonstrated to drive local-scale diversification in which populations split along lines of diet, habitat type, or habitat layer (Ackerly et al., 2006). While climatic factors may be important in determining suitability for each species in the *P. zanzibaricus* complex, it is clear that climatic niche divergence likely cannot explain diversification between these three species alone. According to the sensory drive hypothesis proposed by Génin (2021), the three species of the *P. zanzibaricus* species complex prefer habitats with different acoustic properties that likely may have influenced the evolution of their loud calls. Our study does not show any significant climatic differences between the distribution of these three species. Therefore, we are not able to corroborate the hypothesis of speciation by sensory drive. However, the type of modeling conducted in our study only included climatic variables and therefore cannot capture additional differences in both the abiotic and biotic habitats of the three species that would have likely driven the evolution of their loud calls.

In conclusion, future research should include a more holistic modeling approach that incorporates multiple ecological—both biotic and abiotic—characteristics. Field studies can be conducted to assess habitat use and selection by the three species and the extent to which they display habitat and resource partitioning. We also encourage additional work on population-scale genetic diversity of the three species across their geographic range, as well as potential nonclimatic ecological differences between populations.

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Authors and Affiliations

Evan Miller[1] · Averee Luhrs[1] · Amanda Mancini[2,3] · Mary E. Blair[4] · Luca Pozzi[1]

✉ Luca Pozzi
luca.pozzi@utsa.edu

1   Department of Anthropology, University of Texas at San Antonio, One UTSA Circle, San Antonio, TX, USA

2   Department of Anthropology, The Graduate Center, City University of New York, New York, NY, USA

3   The New York Consortium in Evolutionary Primatology (NYCEP), New York, NY, USA

4   Center for Biodiversity and Conservation, the American Museum of Natural History, New York, NY, USA