

RESEARCH PAPER



Convergent evolution in lemur environmental niches

James P. Herrera 

Duke Lemur Center SAVA
Conservation, Duke University, Durham,
NC, USA

Correspondence

James P. Herrera, Duke Lemur Center SAVA
Conservation, Duke University, Durham, NC
27708, USA.
Email: james.herrera@duke.edu

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Abstract

Aim: To test the hypothesis that adaptive convergent evolution of climate niches occurred in multiple independent lemur lineages.

Location: Madagascar.

Taxon: Lemurs.

Methods: I collected climate and altitude data from WorldClim and summarized the niches of almost all living lemurs (83 species) into phylogenetically controlled principal components. To test for convergent evolution, I searched for multiple, similar climate optima using multi-peak Ornstein–Uhlenbeck models (surface, l1-ou, bayou). I compared the observed level of climate convergence to that simulated under neutral and single-optimum models. To test if behavioural or morphological traits were related to climate niches, I used phylogenetic regressions with activity pattern, diet, and body size.

Results: From an ancestral niche with high rainfall and low seasonality, four lemur lineages independently converged on climate niche optima characterized by high temperatures and low rainfall, supporting adaptive evolution in southwest deciduous and arid habitats. The observed level of convergence was more frequent than expected under Brownian motion and single-optimum simulations, which illustrates that the results are likely not a result of stochastic evolution over long time periods. Nocturnal and cathemeral activity patterns were common among lineages in the arid climate niche.

Conclusion: Lemur climate niche evolution demonstrated that convergence explains the distribution of four independent clades in hot, arid environments of southwest Madagascar. The timing of these convergent shifts coincided with the origination of modern arid-adapted plant genera, some of which are important lemur food sources. These communities have high endemism and are especially threatened by habitat loss. Arid environments are arenas in which convergent evolution is predicted to occur frequently.

KEYWORDS

adaptation, biogeography, desert, ecological divergence, primates

1 | INTRODUCTION

Convergent evolution is a process observed across the tree of life, in which species from independent lineages express similar phenotypes and occupy similar niches (Mahler, Weber, Wagner, & Ingram, 2017). Famous animal examples of convergence include the *Anolis* lizards of the Caribbean islands (Harmon, Kolbe, Cheverud, & Losos, 2005; Losos, Jackman, Larson, Queiroz, & Rodríguez-Schettino, 1998; Mahler, Ingram, Revell, & Losos, 2013; Poe & Anderson, 2019), and cichlids of African Rift Valley lakes (Muschick, Indermaur, & Salzburger, 2012). Species independently evolved preferences for similar habitats and foraging niches in different settings, with concomitant anatomical adaptations to fill those niches. The repeated evolution of analogous traits to similar niches in different clades is strong evidence for adaptive evolution.

Repeated convergence of similar climatic/habitat niches has been identified in many disparate lineages, revealing the importance of abiotic factors in biogeographic evolution. The independent evolution of similar growth forms in plants has long been associated with environmental conditions. For example, similarly shrubby, sclerophyllous vegetation in chaparral environments around the world are composed of multiple evolutionary radiations of plants (Mooney & Dunn, 1970). Convergent mechanisms for cold tolerance evolved among independent lineages of conifers (Yeaman et al., 2016) and angiosperms (Edwards et al., 2017). C4 photosynthesis, a specialized pathway that conserves water, evolved independently among arid savanna grasses (Edwards et al., 2010) and among dicots (Sage, 2004). These examples demonstrate that adaptive phenotypic change can occur in predictable ways due to natural selection; that is, organisms better suited to their niches have higher fitness and populations of these organisms diverge from their ancestral lineage.

Counter to adaptive hypotheses that invoke natural selection, non-adaptive mechanisms including neutral genetic drift and chance can lead to convergence (Losos, 2011; Mahler et al., 2017; Stayton, 2015). Given enough time, independent lineages may converge on similar phenotypes simply by chance. Furthermore, convergence may be due to limited genotypic or phenotypic variation that can be associated with biased mutations and ontogenetic development (Stayton, 2008). To understand the extent to which adaptive convergent evolution has shaped diversity, it is vital to reject the hypothesis of a neutral process.

Madagascar is a mini-continent with diverse tropical habitats characterized by steep climate gradients (Vences, Wollenberg, Vieites, & Lees, 2009). For example, in the southeast one can traverse lowland rainforests, montane cloud forest and arid thickets in a single day (Rakotondranary, Hapke, & Ganzhorn, 2011). Climate, and especially the unpredictability in climate, has been hypothesized to drive the evolution of species' traits and distributions across the fauna and flora of the island (Dewar & Richard, 2007; Ganzhorn, Wright, & Ratsimbazafy, 1999; Wright, 1999). The species richness of ecological communities and the relative abundance of species is driven by climate. While species richness is higher in rainforests than dry forests, abundance is lower in rainforest for lemurs and other

mammals (Ganzhorn, Goodman, & Nash, & Thalmann, 2006; Herrera, 2017a; Stevens & O'Connor, 2006). Changes in the species composition of communities can be explained by changes in elevation, climate and plant productivity (Herrera, 2017a; Kamilar & Muldoon, 2010; Muldoon & Goodman, 2010). Therefore, understanding how climate may drive adaptive ecological divergence can explain how biodiversity evolved in Madagascar.

The lemurs of Madagascar are a diverse group of mammals, with species distributed in nearly all the natural habitats on the island, from rainforests to arid, spiny thicket. Overall, closely related species do not have similar climatic niches; instead, several closely related species show divergent niches (Kamilar & Muldoon, 2010). Examination of individual families showed that within two lineages, the Cheirogaleidae and the Lepilemuridae, there were closely related species that diverged between rainforest and arid environments (Kamilar & Muldoon, 2010). This investigation of phylogenetic signal in climate data for 43 lemur species suggested that closely related species diverged in climate niches as they colonized different habitat types, converging on the climate niches of distantly related species.

Adaptations to hot, dry climates by mammals include changes in activity pattern, body mass, diet and physiology (Degen, 2012; Fuller, Hetem, Maloney, & Mitchell, 2014). It is unclear what traits lemurs may possess that allowed them to colonize the arid biome. Body size in lemurs, for example, was not related to climate variables, and did not follow the classic predictions of Bergmann's rule (Kamilar, Muldoon, Lehman, & Herrera, 2012). Body size evolution appears to be more tightly correlated to diet and activity pattern, with lineages in different niches evolving towards unique optima (Herrera, 2017b). It remains to be tested what traits of lemurs may be adaptations to the environmental niches they occupy.

I tested the hypothesis that independent lineages of lemurs have converged on similar climate niches with associated adaptive evolution in traits, in line with their colonization of the different biogeographic zones of Madagascar. Using climate and phenotypic data on almost all living species from across their geographic ranges, I tested for convergence of different lineages towards similar adaptive 'peaks' in a multi-peak evolutionary landscape. I compared the convergence hypothesis to a non-adaptive, stochastic model of evolution and a single-optimum model. I predicted that variation in traits, specifically in diet, activity pattern and body mass combined, would be related to the climate niche of lemurs because these traits can be adaptive for extracting resources and conserving energy. The results highlight the biogeographic and environmental factors that generated the remarkable diversity of living lemurs.

2 | MATERIALS AND METHODS

2.1 | Study species

Lemurs of Madagascar are an endemic group of primates with about 100 living species (Mittermeier et al., 2010). I used the mean clade credibility tree with 83 species that was inferred using combined morphological and genetic data under a fossilized birth-death



process (Herrera & Dávalos, 2016). To account for uncertainty in the phylogeny, I repeated two of the analyses described below (surface and l1-ou) on 100 trees randomly chosen from the posterior distribution of highly probable trees.

2.2 | Geographic range and climate data

Climate data were taken from the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Data on all 19 variables were extracted from the entire range of species (IUCN range polygons, accessed 2/18/2015) using the 'extract' function in the raster package (Hijmans et al., 2015) for R (R Core Team, 2014). I calculated the mean of each variable, as well as the standard deviation of annual mean temperature and annual mean precipitation. These standard deviations were used to quantify intraspecific variation and account for widespread species that have highly variable climates across their broad range. Variables with intercorrelations greater than $r = |0.90|$ were not included in subsequent analyses, and I chose to include those which represent extremes of seasonality, rather than overall annual means, because the extremes are often the limiting factors in species' ability to persist in an environment (Lynch et al., 2014). The variables that were included in the analyses were isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), temperature annual range (BIO7), precipitation seasonality (BIO15), precipitation of the wettest quarter (BIO16), precipitation of the driest quarter (BIO17), the standard deviation in annual precipitation (standard deviation of BIO12) and altitude. All data were natural log and z-score transformed before further analysis.

2.3 | Species trait data

To test if intrinsic traits of the species can predict the climate niche, I included data on mean body mass, diet (folivore, frugivore, omnivore) and activity pattern (diurnal, nocturnal, cathemeral) that were gleaned from the literature and used in previous analyses (Herrera, 2017a).

2.4 | Analyses

2.4.1 | Phylo-PCA

I used principal components analysis (PCA) to summarize the climate variables into a reduced number of axes based on their intercorrelations using the variance-covariance matrix. Because the data among species are not independent due to the shared evolutionary history of species, I used the phylogenetically corrected PCA (pPCA) with lambda transformation in the R package phytools ('phyl.pca' function Revell, 2009; Revell, 2013). I used these pPCA results to visualize how taxonomic groups partition climate niche space and summarize the multivariate niche for further analyses.

2.4.2 | Testing multi-optima & convergence models

To test for convergent shifts in phenotype among different lineages, I used multi-optima Ornstein–Uhlenbeck (OU) models. OU models include the following parameters: θ (optimum trait value), α (strength of 'attraction' to the optimum) and σ^2 (stochastic evolution, Hansen, 1997). Though these parameters are often interpreted as representing evolutionary processes, they are relative measures. For example, the α values are often interpreted as the strength of selection, constraint around the optimum, or the rate of approach to a new optimum, but α does not necessarily correspond to any of these evolutionary mechanisms. Further, when α reduces to zero, the model of trait evolution is not different from Brownian motion (Cooper, Thomas, Venditti, Meade, & Freckleton, 2016). It is therefore useful to interpret α as the phylogenetic half-life ($\ln(2)/\alpha$), or the time it takes a lineage to reach half the distance from the ancestral state to the optimum, θ (Hansen, Pienaar, & Orzack, 2008). If the half-life is long relative to the age of the clade or tree, then the lineage will not reach that optimum in a realistic time and there is weak attraction to that optimum (Cooper et al., 2016).

I used three different analyses that search for shifts in optima across the tree: the 'surface' (Ingram & Mahler, 2013), 'l1-ou' (Khabbazian, Kriebel, Rohe, & Ané, 2016), and 'bayou' methods (Uyeda & Harmon, 2014). All three analyses search for shifts in optima in the OU model, and varied in their statistical performance and power (Khabbazian et al., 2016). The bayou analysis was the most conservative, having low false positive rates but low power to detect true shifts, while the surface analysis was the most likely to detect true shifts but also had high false positive rates. The l1-ou approach had intermediate performance, consistently identifying true shifts while minimizing false positives (Khabbazian et al., 2016). While surface and l1-ou approaches can incorporate multiple traits simultaneously to identify multivariate shifts, bayou cannot which can also limit its power to detect shifts in multivariate niche space.

The first method, surface, is a maximum likelihood approach that searches for the number and location of convergent regimes on a phylogenetic tree given uni- and multidimensional trait data (Ingram & Mahler, 2013). The surface search algorithm starts with a single OU process and estimates parameter values and the sample size-corrected Akaike Information Criterion (AICc). The algorithm iteratively adds unique optima at different nodes of the tree and compares the likelihood of the models with multiple optima to the simpler OU models using AICc; if the AICc value is improved, the model is retained for the next step, and if not the additional peak is collapsed, and new shift configurations are examined. To test for convergence, a backwards phase collapses shift configurations with similar optima into a single shift and compares the AICc of that new configuration to that with multiple shifts. If AICc is improved, convergence on the same optimum is inferred. A single α and σ^2 parameters are used for all optima to reduce the complexity of models. The AICc threshold for adding OU models was set at 2 in these

TABLE 1 Summary of phylogenetic principal components analysis

Variable	pPC1	pPC2	pPC3
Isothermality (daily temperature range/annual temperature range × 100)	0.22	0.88	0.25
Temperature seasonality (SD × 100)	−0.90	−0.21	−0.10
Maximum temperature of the warmest month	−0.78	0.55	0.07
Minimum temperature of the coldest month	0.87	0.38	0.20
Temperature annual range	−0.66	−0.25	−0.55
Precipitation seasonality (coefficient of variation)	0.68	−0.61	−0.19
Precipitation of the wettest quarter	−0.49	−0.63	0.51
Precipitation of the driest quarter	0.04	−0.90	0.40
Standard deviation in annual precipitation	0.84	−0.26	−0.12
Altitude	0.64	−0.15	−0.26
Total variance	44.77%	30.07%	9.54%

Note: The loadings of the original variable on each PC axes are given as well as the proportion of variance in the data summarized by the component.

analyses (Burnham & Anderson, 2002; Ingram & Mahler, 2013). I ran the surface analysis using the R package surface, and assessed the number of convergence events based on the ‘c’ and ‘k’ convergence’ statistics. The c statistic measures the number of niche shift events to the convergent optimum occupied by multiple lineages, and k’ convergence measures the number of convergent optima reached by multiple shifts (Ingram & Mahler, 2013). One advantage of the surface analysis is that it can model the evolution of multiple traits simultaneously, representing multidimensional niches. I ran surface with pPC1 – 3 analysed together.

To determine the number of convergence events expected under a neutral drift model and a single-optimum model, I simulated trait data with the parameters of the observed data (mean and standard deviation) under a Brownian motion and single-optimum OU model of evolution using surface. I ran the surface model on 1,000 simulated traits and recorded the number of convergent regimes (k’ statistic) and the number of shifts to convergent regimes (c statistic). I then compared the observed frequency of shifts for the empirical data to the frequency distribution of the number of shifts derived from the analysis of the simulated data.

The second approach, l1-ou, uses maximum likelihood and the statistical lasso technique to optimize the number and value of parameters in the overall model: α , σ^2 and number, location and magnitude of multiple θ parameters. The statistical lasso technique reduces the number of shifts estimated through a regularization parameter that weights multiple shift configurations to improve the likelihood of the model, thus penalizing complex models (multiple

shift configurations) by assigning a weight of 0. Like surface, l1-ou can analyse multiple traits simultaneously, and pPC1 – 3 were analysed together. Also like surface, l1-ou can be used to judge which climate niches are convergent by determining which have statistically similar θ values and collapsing them. I ran the l1-ou models using the phylogenetic Bayesian Information Criterion (pBIC), which is a more stringent penalization of highly parameterized models than AICc, and also accounts for phylogenetic covariance. The pBIC was found to have the highest precision in number and location of simulated shifts, but the lowest recall of all true shifts for multiple analyses and information theoretic criteria (Khabbazian et al., 2016). To determine the confidence in climate niche shifts, I used the nonparametric bootstrap technique that draws the phylogenetically controlled trait covariance randomly with replacement 100 times to quantify the number of shifts that were supported in permuted datasets.

The bayou analysis seeks to identify independent adaptive regimes using a Bayesian framework, with a reversible-jump Markov chain Monte Carlo (MCMC) algorithm (Uyeda & Harmon, 2014). Though the philosophy of the method is similar – to search for unique peaks on a rugged adaptive landscape – the bayou analysis does not specifically determine convergent and nonconvergent regimes. Also, unlike surface and l1-ou, bayou does not analyse trait evolution with multiple traits simultaneously; instead, scores for each pPC axis were analysed in separate steps. I ran two independent chains of one million generations using weakly informative priors (α and σ^2 = half Cauchy, dsb allowing 1 shift per branch and equal probabilities of shifts among branches, the number of shifts between five and 200, θ = mean and standard deviation of observed data). The standard error was assigned based on the observed data. The first 30% of generations were excluded as burn-in. I determined that runs were stationary using effective sample size estimates >200, and that runs converged based on Gelman and Ruben R statistic with values ~1 (Uyeda & Harmon, 2014).

2.4.3 | Phenotypes

To test the hypothesis that lemur traits covary with climate, I used the data on activity pattern, diet and body mass (natural log transformed) for the lemur species in this set, which coded species as diurnal, nocturnal, or cathemeral, and folivorous, frugivorous and omnivorous (Herrera, 2017a). I used phylogenetic generalized least squares (PGLS) regression to test the hypothesis that lemur traits predict the climate PC axes. PGLS models with correlation structures based on Brownian motion, Pagel’s lambda and Martins alpha transformations were compared using AIC to determine which model best fit the data (nlme and ape packages, Paradis, Claude, & Strimmer, 2004; Pinheiro, Bates, DebRoy, & Sarkar, 2017).

3 | RESULTS

The first three pPC axes were retained based on decreasing variance represented by subsequent axes (Table 1; Figure 1). The first axis

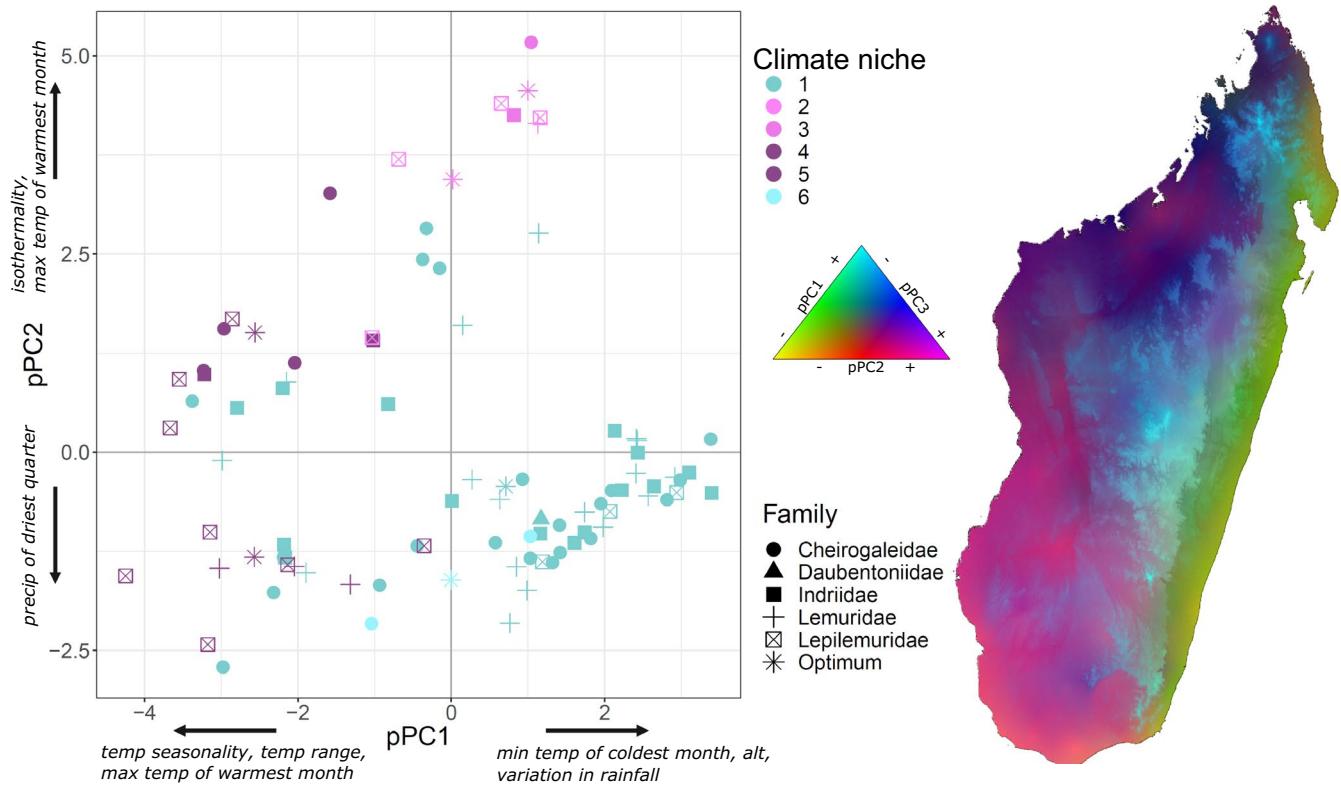


FIGURE 1 Distribution of lemur species in six climate niches inferred from the surface analysis. Colours correspond to the map of Madagascar, highlighting areas with similar climate variables based on principal components analysis (PCA). Coloured map is based on the first three PC axes from a geospatial PCA of the same WorldClim variables as used in the phylogenetic PCA, and coloured according to a red-green-blue spectrum (rasterPCA function in the raster package). The colours in the scatterplot are meant to represent the colours in the map to illustrate where the convergent species are found

summarized 44.77% of the variance in the data, and largely separated species with greater standard deviation in annual precipitation, higher elevation and higher minimum temperature of the coldest month (positive values) from species with greater temperature seasonality, range and higher temperature in the warmest month (negative). The second axis summarized 30.01% of the variance and was largely correlated with the isothermality and residual variation in maximum temperature of the warmest month (positive), and those species with higher precipitation in the driest quarter (negative). The third axis summarized 9.54% of the variance and largely captured residual variance in climate, especially precipitation in the driest quarter. Other axes summarized much less variance in the data and were not examined. Subsequent analyses focused on the first three axes. The lambda value, which measures the phylogenetic signal in the data, was <0.001 , indicating closely related species do not have similar climate data.

The results of the surface analysis revealed that there were 11 shifts towards six unique climatic niches (Figure S1). There were three unique climate niches to which lineages shifted independently nine times, which is consistent with convergent evolution towards these climate niches (Figure 1). Three climate niches were unique shifts with no convergences. These results were consistent across the 100 trees in the posterior distribution, with median values of 8 shifts (48% of trees) to 3 (61% of trees) convergent climate niches

(Figure S2; Table S2). The number of convergent niches and shifts to convergent niches in the observed data was within the range of those simulated under Brownian motion. Under a simple Brownian motion model, 51.4% of simulations had fewer than three convergent niches, and 84.8% had fewer than nine shifts towards those convergent regimes (Figure S3). In all simulations under a single OU process, there were four shifts to two convergent niches.

The background climate optimum (1 in Table 2) is characterized by high positive values on pPC1, moderately negative values on pPC2, and weakly negative values on pPC3. These axes translate to

TABLE 2 Optimal climate niche values (θ) for each environmental regime identified by the surface analysis

Climate niche	pPC1	pPC2	pPC3
1	0.71 (0.61)	-0.43 (-0.37)	-0.04 (-0.01)
2	0.02 (0.02)	3.44 (3.44)	-0.28 (-0.28)
3	1.00 (1.00)	4.57 (4.52)	-1.68 (-1.55)
4	-2.57 (-2.57)	-1.32 (-1.32)	-0.74 (-0.75)
5	-2.56 (-3.15)	1.51 (1.30)	1.47 (1.75)
6	-0.005 (-0.005)	-1.61 (-1.61)	2.15 (2.14)

Note: Numbers in parentheses are the median values from analysis of 100 trees from the posterior distribution of trees. Cells in bold are the convergent climate niches.

low temperature seasonality and moderate temperatures, moderate rainfall seasonality and high precipitation especially in the driest months. Three lineages independently converged on a similar optimal climate niche characterized by near-zero values on pPC1, high positive values on pPC2, and high negative values on pPC3. This climate niche was characterized by high temperatures, low precipitation and low seasonality (Climate niche 3 in Table 2; Figure 2). The three convergent lineages were *Lemur catta*, *Propithecus verreauxi* and *Microcebus griseorufus* (Figure 2).

The second convergent climate niche (4 in Table 2) had two independent lineages with shifts towards negative values on pPC1, 2, and 3. This niche had high seasonality, high temperatures in the warmest months and high precipitation in the driest months. The lineages included the *Lepilemur* and *Eulemur* clades from the far north of Madagascar. The third convergent climate niche (5 in Table 2) had four independent lineages that shifted towards negative values on pPC1 and positive values on pPC2 and 3. These dimensions were characterized by high seasonality and temperatures, low annual precipitation but high precipitation in the wettest quarter. Lineages that shifted towards this niche included clades from the genus *Lepilemur*, *Microcebus* and *Avahi* from western Madagascar. Two other unique climate niches were identified by the surface analysis, though these differed by only small degrees

from either the hot arid niche (2 in Table 2) or the background niche (6 in Table 2, Figure 1).

The α values were relatively high and the associated phylogenetic half-life was short relative to the age of the lineages (Table 3), indicating that the time it would take to reach the new optimum is short compared to tree height. The σ^2 values were generally higher for pPC1 than pPC2 or 3, illustrating greater variance in evolution of climate variables associated with pPC1 than those with pPC2 or 3.

The I1-ou approach identified fewer shifts than surface (Figure 2). The shifts supported by I1-ou included similar clades with shifts towards climate niches 2, 3 and 4 in Table 2, with high temperatures, low precipitation and low seasonality. The same species of *Microcebus*, *Lemur* and *Propithecus* were identified, in addition to the subclade of the genus *Lepilemur* that surface found in its own climate niche (2 in Table 2). The convergent shifts had high support based on the nonparametric bootstrap (Figure 2). The values of the optimal climate niches were similar to those found by surface for climate niche 3 (Table S3) and were stable across the 100 trees from the posterior distribution (Table S4).

The bayou analysis identified a mean number of climate niche shifts of 3.59 ($SD = 1.86$) for pPC1, 5.06 ($SD = 2.20$) shifts for pPC2 and 5.49 shifts ($SD = 2.41$) for pPC3 (Table S5). In contrast to the results from the surface and l1-ou analyses, the bayou analysis

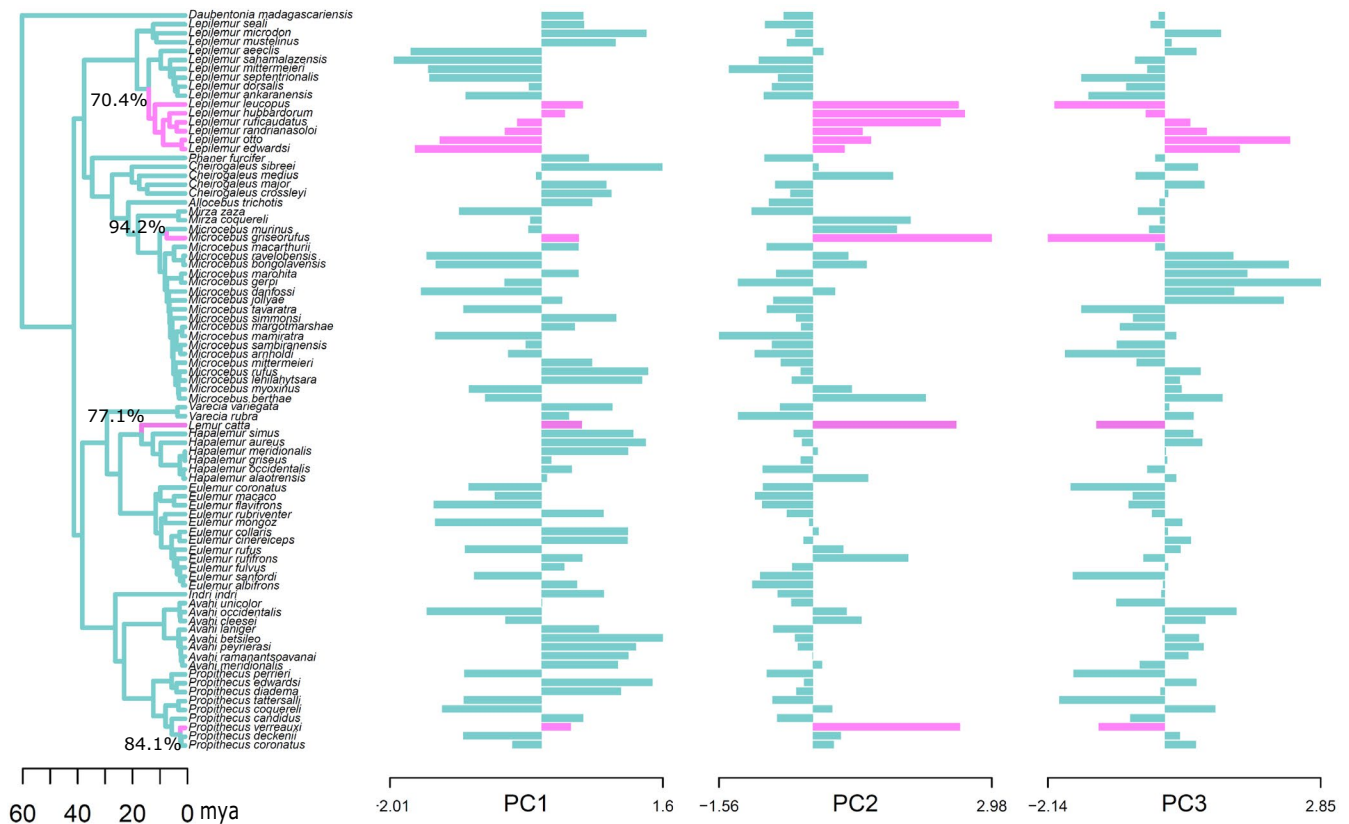


FIGURE 2 Tree with unique climate niche regimes coloured according to the results of the I1-ou analysis. Lineages with branches in pink represent similar convergent adaptive climate niches corresponding to the color-coded map in Figure 1, while lineages in blue had the ancestral climate niche (see Table 2). Numbers at nodes indicate the support for the shift based on a nonparametric bootstrap approach. The bar-plots depict the values of the climate pPCs, with those in pink identified as convergent optima in the I1-ou model

resulted in weak posterior probabilities for specific shifts. The subclade of *Lepilemur* that surface and l1-ou identified as convergent in climate niche were also detected by bayou as having a uniquely high temperature, low precipitation and seasonality, though with low posterior probability of a shift (Figure S4). The weak signal for convergence events in the bayou analysis may be due to the way in which bayou can incorporate variation within species in the analysis, but may also be due to the low statistical power of the method.

3.1 | Phenotypes

The PGLS models showed that diurnal species had significantly lower scores on pPC1 and pPC2 than cathemeral or nocturnal species, but not on pPC3 (pPC1, diurnal coefficient = -1.46 , $t = -2.70$, $p = .009$; pPC2, coefficient = -0.87 , $t = -2.07$, $p = .04$). No other traits were significantly related to climate PCs (Table S6). The Martins alpha transformation for branch lengths was consistently a better fit to the data than the Pagel's lambda or Brownian Motion transformations ($\Delta AIC > 5$ in all tests). Alpha values were consistently high, showing low phylogenetic signal in the climate pPC data.

4 | DISCUSSION

In this study, I found that four lineages of lemurs independently shifted from an ancestral niche in rainforests to hot, arid habitats. The observed level of convergence was higher than expected by stochastic or single-optimum processes. Lemurs in hot, arid habitats tended to be nocturnal or cathemeral. These results are consistent with the hypothesis of convergent evolution in lemur climate niches, and shed new light on the biogeographic evolution of Malagasy fauna.

The biogeographic processes that led to species diversity and distributions on Madagascar have been an unresolved debate for decades. The marked contrasts among climate zones were hypothesized to drive the biogeographic divergence of species and communities among eastern rainforests, western dry deciduous forests and arid spiny thicket (Muldoon & Goodman, 2010). River barriers may have also created allopatric separation among species, and refugial hypotheses invoke Pleistocene climate change and range contraction within watersheds as causes of speciation and distribution (Pastorini, Thalmann, & Martin, 2003; Wilmé, Goodman, & Ganzhorn, 2006). Lemur species from different taxonomic families had considerable overlap in climate dimensions, which led to the hypothesis of frequent convergent evolution in climate niches (Kamilar & Muldoon, 2010). The results of this study support independent evolution of climate niches in western and southern dry forests from an ancestral niche in eastern rainforests.

There is mounting evidence for a general trend of biogeographic shifts from rainforest to dry forest across species in Madagascar. Similar to lemurs, tenrecs also transitioned from rainforests to dry forests (Everson, Olson, Soarimalala, & Goodman, 2016), and leaf chameleons showed several independent divergence events in

TABLE 3 Parameters of the best fitting multi-peak Ornstein–Uhlenbeck (OU) model

Parameter	pPC1	pPC2	pPC3
α	1,600, 0.35, 0.47	2.24, 0.67, 1.39	0.76, 0.32, 0.76
Phylogenetic half-life	<0.001, 1.98, 1.47	0.31, 1.03, 0.50	0.91, 2.17, 0.91
σ^2	8,623.40, 3.14, 3.89	4.83, 2.07, 5.87	0.80, 0.54, 1.17

Note: α = strength of selection, phylogenetic half-life = time to reach optimal niche value in millions of years, σ^2 = stochastic variation in niche value over time, or evolutionary rate. The three values in each cell represent the results of the surface, l1-ou, and the bayou models, respectively.

which clades split between eastern and western domains (Townsend, Vieites, Glaw, & Vences, 2009). In orchids (Genus *Bulbophyllum*), biogeographic distributions were explained by high transition rates between eastern and western domains, and shifts from ancestral niches in lowlands to high elevations in the central plateau (Gamisch, Fischer, & Comes, 2016). Reptiles and amphibians have peaks of species richness in the rainforests, and similar to lemurs, the southwest is an area of endemism for some reptile groups (Brown, Cameron, Yoder, & Vences, 2014). These concordant patterns across species point to the role of the eastern rainforests as sources of diversity, and transitions to western and southern dry forests to explain biogeographic patterns in Madagascar.

The role of the central highlands as a dispersal barrier between the east and west has figured prominently in debates about Madagascar biogeography. The highlands are predominantly mixed anthropogenic landscapes, with agricultural fields, pastures, grasslands, exotic tree plantations and human settlements. Despite the current denuded state of the central highlands, remaining patches of natural vegetation and the paleoecology leave a signature of forested habitat in the Holocene (Burney et al., 2004; Ganzhorn et al., 2006). The Pleistocene highlands were cold and dry, consisting mostly of shrub, grass and heath vegetation, but there was a distinct shift to woodland/savanna mosaic during warm, moist conditions after the last glacial maximum (Burney et al., 2004). The paleoecology of sites in the central western highlands indicates it was a wooded marsh with ~20 sympatric, forest-dwelling lemur species, hippos and other humid forest elements (Crowley, Godfrey, & Irwin, 2011; Godfrey & Jungers, 2003). Several modern highland fragments with both wet and dry forest characteristics may be relicts of a pre-human mosaic landscape (Ganzhorn et al., 2006). The repeated transitions from eastern rainforest to western and southern dry forest observed in this study indicate dispersal events, supporting hypothesized connectivity in the past. The evidence for past connectivity between the east and west refutes the long-standing hypothesis of a hard barrier between the two.

The arid environments of southern Madagascar may be relicts of a formerly widespread biome during the Cretaceous that has been contracting since the Eocene. After the Eocene, the climate in



Madagascar became increasingly wetter as it moved above the arid subtropical zone (30° south latitude) and the northward movement of India allowed the trade winds of the Indian Ocean to bring moisture (Buerki, Devey, Callmender, Phillipson, & Forest, 2013; Wells, 2003). Alternatively, the distribution of climate regimes seen today may have been relatively stable in deep time, though cooler and with less distinct precipitation gradients and seasonality than today (Ohba, Samonds, LaFleur, Ali, & Godfrey, 2016). Despite the antiquity of arid climates in Madagascar, the extant lemur lineages that converged on the hot, arid niche diverged between 15 and 2 mya. During this wide temporal window, global climates generally transitioned from warm, moist conditions in the mid-Miocene to widespread aridification during the end-Miocene and Plio-Pleistocene (Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The shift in global climate may have been a driving factor in the expansion and diversification of arid-adapted taxa.

Similarly, approximately half of the modern arid-biome plant taxa diversified after the mid-Miocene (~15 mya), with several genera originating in the Plio-Pleistocene, including within the endemic superfamily Didiereoidea (Buerki et al., 2013). One genus in particular, *Alluaudia*, is an important food source for at least two of the arid-adapted lemurs, *L. catta* (Simmen et al., 2006) and *L. leucopus* (Dröscher & Kappeler, 2014). Thus, the transition to the arid biome by lemur lineages largely coincided with the diversification of arid-adapted plants. Future research should investigate the role of climate change through deep time in the concordant evolution of Madagascar's flora and fauna.

The evolutionary history of Madagascar's biodiversity is difficult to reconstruct given the lack of Cenozoic fossil record. The unique species that have gone extinct just in the last 2,000 years illustrate even higher rates of endemism and diversity than we see today, including more than 17 giant lemurs (Goodman & Jungers, 2014). The number of convergent events towards the hot, arid climate niche inferred in this study would likely have been higher if the extinct lemurs were included, because at least four different lineages co-existed with extant lemurs in the south (Crowley et al., 2011). The climate of the south was also hot and dry 2,000 years ago (Crowley et al., 2017). Several of the extinct species were eating C_4 photosynthesizing plants, pointing to an open, hot, arid habitat (Crowley & Godfrey, 2013). I could not include the subfossil species in this analysis for several reasons. First, the known localities for subfossil species are a subset of their actual extent of occurrence, and so the level of precision for the extant and extinct lemur ranges were not comparable. Most of these localities are concentrated around the western coasts, where sedimentary rock or limestone caves have allowed for deposition and recovery of subfossil remains (Godfrey, Jungers, & Burney, 2010; Goodman & Jungers, 2014). Further, there is uncertainty in the species designation for some subfossil taxa at their range extremes, making geographic limits difficult to ascertain (Godfrey et al., 2010). Lastly, though reconstructions of Holocene climate are available, they are subject to great uncertainty and low resolution for this particular question (Braconnot et al., 2012). Despite these limitations, modelling the changes in evolutionary climate trajectories from the near-recent

past to the present incorporating the extinct lemurs would clarify if and how lemurs have responded to past climate change.

Analogous phenotypic adaptations in morphology, physiology and behaviour in response to similar habitats typify convergent evolution (Ord & Summers, 2015). Colonizing xeric environments is limited by adaptations to extract and conserve water and tolerate high temperatures. Nocturnal and cathemeral activity patterns are adaptive for avoiding diurnal heat stress and conserving water and energy by being active during the cooler diel period (Fuller et al., 2014; Schmidt-Nielsen, 1975; Schmidt-Nielsen & Schmidt-Nielsen, 1952). Heterothermy (i.e., torpor and hibernation) is similarly adaptive for conserving energy and water in tropical environments (Dausmann, Glos, Ganzhorn, & Heldmaier, 2004; Kobbe & Dausmann, 2009; Kobbe, Ganzhorn, & Dausmann, 2011). Heterothermy and nocturnal or cathemeral behaviours are adaptations observed in multiple independent lineages of desert adapted rodents (Mares, 1976). The analysis of traits in this study showed that species in the arid climate niches tended to be nocturnal or cathemeral, including a clade within the genus *Lepilemur* and *M. griseorufus*. *Lepilemur* and *Microcebus* species use tree holes for day nests and rely on large trees, which are more insulating than small trees and alleviate heat stress (Rakotomalala, Rakotondraparany, Perofsky, & Lewis, 2017; Schmid, 1998). This nest-preference behaviour possibly allows the arid-adapted species to conserve water and energy that would otherwise be lost in thermoregulation. *Microcebus* use seasonal torpor to save energy during the long dry season (Kobbe & Dausmann, 2009; Kobbe et al., 2011). Though *Lepilemur* does not exhibit heterothermy, they have extremely low basal metabolic rates and their thermoneutral zone fluctuates with seasons to save energy (Bethge, Wist, Stalenberg, & Dausmann, 2017). Two species in the arid south, *L. catta* and *P. verreauxi*, are predominantly diurnal, though *L. catta* has recently been shown to be cathemeral (LaFleur et al., 2014; Parga, 2011). *L. catta* is well known for its flexible habitat use and ability to thrive in extremely harsh environments, though they cannot persist far from permanent water sources (Sauther, Sussman, & Gould, 1999). *P. verreauxi* in these arid habitats have never been observed to drink water (Simmen, Hladik, & Ramasiarisoa, 2003), and apparently meet all their water needs from their diet and dew on leaves. These behaviours may have allowed the four lineages to adapt in the harsh arid environment of the southwest.

Physiological adaptations are also important to survival and fitness in arid habitats (Fuller et al., 2014). In primates, increases in glycogen content and capillarization of the sweat glands are positively correlated with temperature and negatively related to precipitation, indicating that adaptations in skin physiology are also associated with climatic niches, though data are limited for lemurs (Best & Kamilar, 2018). Desert rodents have exceptionally long nephridia in their kidneys which allow them to extract water that would otherwise be lost in urine (Costa, Houser, & Crocker, 2013). Another avenue of future investigation should examine kidney physiology in primates. Little research has been conducted on kidney form and function in primates generally (e.g., Raharison, Mogenicato, & Sautet, 2009; Straus, 1934), and even less has been done to compare kidney

physiology in relation to habitat type. Further physiological research would clarify the proximal adaptations that allow these lemur species to persist in hot arid environments.

Convergent evolution in physiognomy, physiology and behaviour in response to arid climates is observed in many communities of similarly adapted organisms from disparate parts of the evolutionary tree. The repeated independent evolution of sclerophyllous, shrubby vegetation in Mediterranean-like climates around the world (Mooney & Dunn, 1970), and succulent, water-conserving plants in desert climes (Arakaki et al., 2011) are clear examples of how limitations set by the climate drive evolution of similar physiological and morphological adaptations in distantly related lineages. Similarly, adaptations to desert environments such as nocturnality, bipedality and large ears are convergent in distantly related rodent lineages (Mares, 1975, 1980). The arid biomes across the globe are thus biological arenas in which convergent evolution is predicted to be highly prevalent.

Though convergence is often associated with adaptive evolution in response to selection (Moen, Morlon, & Wiens, 2015), other mechanisms can explain the pattern, including chance. The appearance of a pattern consistent with convergence may occur through genetic drift over long periods and/or due to constraint in the available trait space (Mahler et al., 2017; Stayton, 2015). To understand the causes and consequences of convergent evolution, it is necessary to compare these alternative possibilities (Mahler et al., 2017). In this study, convergent evolution was more frequent than expected by random processes, showing that the observed patterns are not consistent with random accumulation of variance in climate niches. The results of the simulation showed that, given the long time period of lemur evolution, convergent evolution can occur even under a stochastic, nondeterministic model of trait evolution. Under a stochastic or single-optimum model, convergence was expected less frequently than observed, though even under simpler models at least two convergence events would be expected. It is difficult to ascertain from these data if species are truly adapted to the arid niche, however, because sympatry in the southern spiny forest may be the result of recent biogeographic events, such as dispersal. Thus, further research is needed to understand the extent of adaptation to the hot, arid zone. The limited number of convergences observed illustrates two main points about lemur biogeography: (a) the higher species diversity in the rainforests, and (b) the limitations associated with the evolution of physiological adaptations to tolerate new climate regimes.

This study showed the unique evolutionary history represented by the convergent lineages in southern arid forests. These habitats are unique, with high local endemism and diversity despite the harsh environment. Unfortunately, southern and western dry forests are under heavy pressure from anthropogenic forces, including burning for pasture and agriculture, and the dry environment promotes the spread of fire (Waeber et al., 2015). While all habitats are threatened by forest loss, the southern and western forests are among the most severely fragmented and most quickly disappearing (Harper, Steininger, Tucker, Juhn, & Hawkins,

2007; Vieilledent et al., 2018). It is imperative to protect the last remaining pockets of these rich habitats, which have been a living laboratory of evolutionary forces leading to unparalleled levels of endemism.

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DATA AVAILABILITY STATEMENT

All data were deposited in the Dryad Data Repository (<https://doi.org/10.5061/dryad.cjsxksn1n>).

ORCID

James P. Herrera  <https://orcid.org/0000-0002-0633-0575>

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BIOSKETCH

James P. Herrera is a research scientist at Duke University with interests in biogeography, macroevolution and applications to conservation biology, with a special focus on Madagascar.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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