

The Climatic Niche Diversity of Malagasy Primates: A Phylogenetic Perspective

Jason M. Kamilar^{1,2*}, Kathleen M. Muldoon^{3,4}

1 Department of Anthropology, Yale University, New Haven, Connecticut, United States of America, **2** Yale Molecular Anthropology Laboratory, Yale University, New Haven, Connecticut, United States of America, **3** Department of Anatomy, Dartmouth Medical School, Hanover, New Hampshire, United States of America, **4** Department of Anthropology, Dartmouth College, Hanover, New Hampshire, United States of America

Abstract

Background: Numerous researchers have posited that there should be a strong negative relationship between the evolutionary distance among species and their ecological similarity. Alternative evidence suggests that members of adaptive radiations should display no relationship between divergence time and ecological similarity because rapid evolution results in near-simultaneous speciation early in the clade's history. In this paper, we performed the first investigation of ecological diversity in a phylogenetic context using a mammalian adaptive radiation, the Malagasy primates.

Methodology/Principal Findings: We collected data for 43 extant species including: 1) 1064 species by locality samples, 2) GIS climate data for each sampling locality, and 3) the phylogenetic relationships of the species. We calculated the niche space of each species by summarizing the climatic variation at localities of known occurrence. Climate data from all species occurrences at all sites were entered into a principal components analysis. We calculated the mean value of the first two PCA axes, representing rainfall and temperature diversity, for each species. We calculated the *K* statistic using the Physig program for Matlab to examine how well the climatic niche space of species was correlated with phylogeny.

Conclusions/Significance: We found that there was little relationship between the phylogenetic distance of Malagasy primates and their rainfall and temperature niche space, i.e., closely related species tend to occupy different climatic niches. Furthermore, several species from different genera converged on a similar climatic niche. These results have important implications for the evolution of ecological diversity, and the long-term survival of these endangered species.

Citation: Kamilar JM, Muldoon KM (2010) The Climatic Niche Diversity of Malagasy Primates: A Phylogenetic Perspective. PLoS ONE 5(6): e11073. doi:10.1371/journal.pone.0011073

Editor: Sharon Gursky-Doyen, Texas A&M University, United States of America

Received: April 22, 2010; **Accepted:** May 19, 2010; **Published:** June 11, 2010

Copyright: © 2010 Kamilar, Muldoon. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: The authors have no support or funding to report.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: jason.kamilar@yale.edu

Introduction

With the development of advanced quantitative tools, researchers are now well positioned to examine biological variation in an evolutionary context. This is especially true for behavioral and ecological characteristics, with many ecologists now using an explicitly evolutionary approach to examine ecological diversity [1,2]. It has become widely accepted that closely related species occupy similar ecological niches, and that these niches diverge as the evolutionary time between species increases [3,4,5,6]. Several recent studies, for example, of Costa Rican plants [7] and Neotropical frogs [8], have supported this pattern. However, different evolutionary scenarios may yield contrasting results [9]. For instance, several authors have argued that there should be little relationship between niche similarity and phylogenetic distance in situations where the rate of evolutionary divergence is higher early in a clade's history than later on, such as occurs in adaptive radiations [1,9,10,11]. This hypothesis is supported by several studies of *Anolis* lizards in the Caribbean, where closely related species occupy divergent niches [12,13]. The ubiquity of this pattern of phylogenetic signal is currently unknown.

Phylogenetic signal has most recently been defined as the degree to which any trait is correlated with a phylogeny [1,14]. Strong phylogenetic signal is defined as a significant correlation between the degree of relatedness among species and their biological similarity, with trait similarity decreasing as phylogenetic distance increases. This pattern is potentially due to constant-rate genetic drift. [1,9]. Alternatively, weak phylogenetic signal may result from divergent selection [1,9].

In this study, we test the hypothesis that there is phylogenetic signal in the climatic niche of Malagasy primates. We first quantify the climatic niche space of Malagasy primates based on known localities of species occurrence and GIS climate data using an ecological niche modeling approach. This approach provides a quantitative summary of species' climatic niches that is amenable to statistical analysis and summarizes their known climatic tolerances. Phylogenetic analyses have demonstrated that lemurs evolved by adaptive radiation following a single colonization event to Madagascar [15,16]. Today, lemurs inhabit nearly every possible climatic and habitat niche in Madagascar, from the highly seasonal, arid spiny deserts of the south, to the aseasonal, humid evergreen rainforests of the east [17]. If closely related

Table 1. Results of the first two principal components summarizing the climatic niche space of Malagasy primates.

Variable	Factor Loadings	
	Factor 1	Factor 2
Log Annual Mean Temp.	0.706	0.426
Log Isothermality	0.287	0.618
Log Temp. Seasonality	-0.194	-0.951
Log Temp. Annual Range	0.542	-0.743
Log Annual Precip.	-0.745	0.547
Log Precipitation Driest Month	-0.868	-0.077
Log Precipitation Seasonality (CV)	0.761	0.156
Log Precipitation Warmest Quarter	-0.829	0.279
Log Altitude	-0.590	-0.327
Eigenvalue	3.836	2.533
Proportion of variance explained	0.426	0.281

doi:10.1371/journal.pone.0011073.t001

species occupy distinct climatic niches, then we expect to find weak phylogenetic signal in the climatic niche space of Malagasy primates as a whole.

Understanding ecological diversity in a phylogenetic context is critical because the assumption that there is a close relationship between ecological and evolutionary similarity is at the foundation of a wide range of biodiversity research, including ecological niche modeling of species ranges in the future [1,2,18]. Systematically testing this potential relationship will help us understand the possible future diversity of species. This is especially important for Malagasy primates, as they are a highly diverse and threatened group of vertebrates [19,20].

Results

The PCA analysis produced nine components, with the first two accounting for over 70% of the total variance in the original dataset. Four variables related to rainfall patterns loaded heavily on the first principal component: 1) mean annual rainfall (-), 2) precipitation seasonality (+), 3) precipitation in the driest month (-), and 4) precipitation in the warmest quarter (-). Two variables related to temperature variation loaded heavily on the second principal component: 1) temperature seasonality (-) and 2) temperature annual range (-) (Table 1).

By examining the first two components in a bivariate plot (Figs. 1–5), several ecological patterns are revealed. Each quadrant of the graph captures sites that exhibit a unique combination of annual rainfall, rain seasonality and temperature seasonality. The lower right quadrant of the plot represents localities with relatively

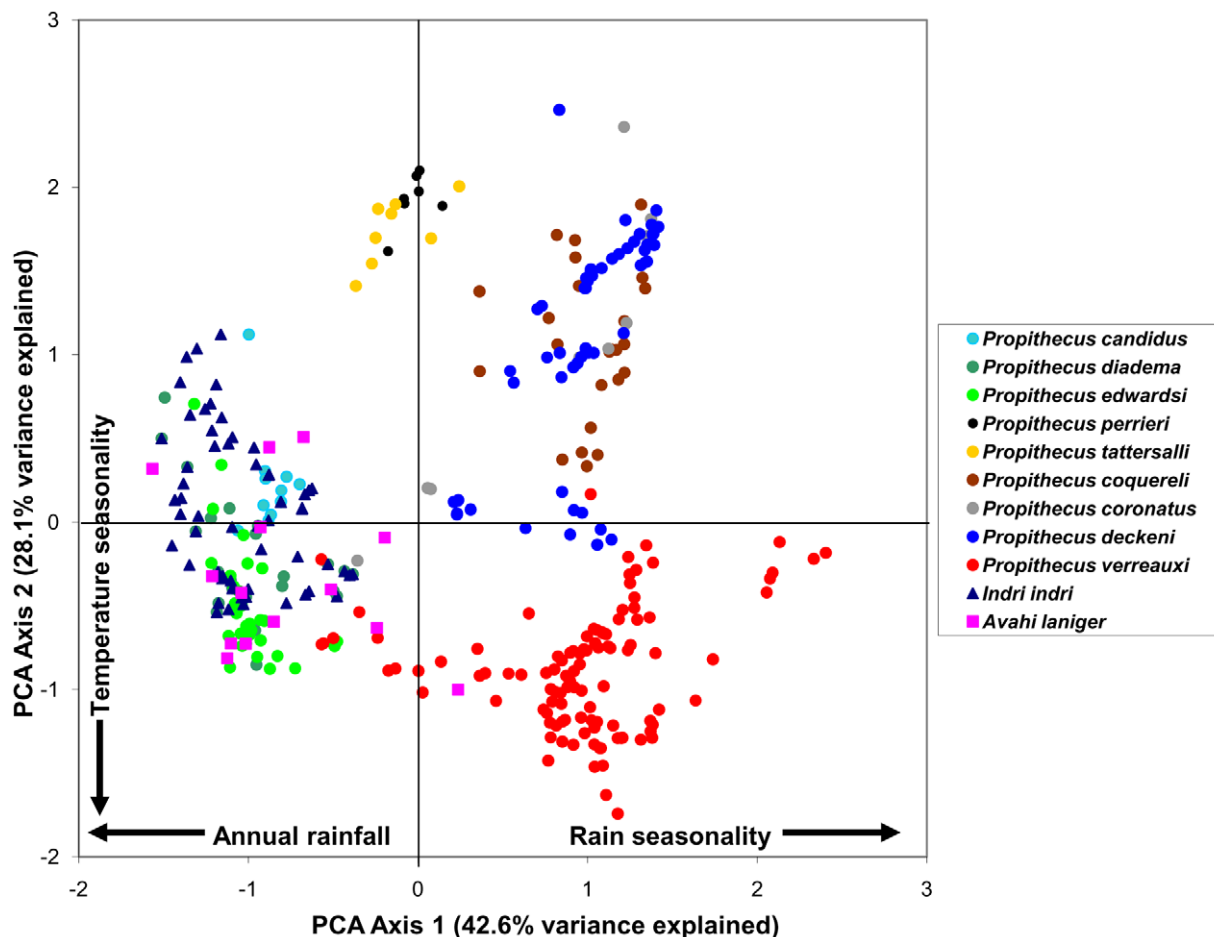


Figure 1. Plot of PCA scores representing the multivariate climatic niche space of Indridae species based on their known localities. The plot illustrates the same multivariate space as figures 2–5.
doi:10.1371/journal.pone.0011073.g001

high levels of seasonality in both mean annual rainfall and temperature, such as localities of the spiny thicket of southern Madagascar (e.g. Beza Mahafaly Special Reserve). Alternatively, sites in the lower left quadrant exhibit high temperature seasonality, but lower levels of rain seasonality (corresponding with high annual rainfall). Many of these sites are found in the humid evergreen forests of eastern Madagascar, such as Ranomafana National Park. Furthermore, plots of the PCA scores revealed high levels of climatic niche space diversity within several genera, especially those containing numerous species (Figs. 1–5). For example, *Propithecus*, *Eulemur*, and *Microcebus* occupy nearly all possible environmental niche spaces as defined by the variables and taxa included in this study. In contrast, members of less diverse genera such as *Varecia* and *Indri* occupy relatively narrow niches.

We found no significant phylogenetic signal in the first two climatic niche axes, regardless of the taxonomic group analyzed. For all Malagasy primates (n=43), we found no significant phylogenetic signal in PC1 ($K=0.294$, $p=0.116$), which is related to rainfall patterns (Fig. 6) or in PC2 ($K=0.245$, $p=0.429$), which is related to temperature variables (Fig. 7). Patterns of phylogenetic signal were similar at the family level, except for the indriids. Significant phylogenetic signal was absent in the rainfall and temperature niche axes for both the cheirogaleids (PCA 1: $K=0.265$, $p=0.836$ and PCA 2: $K=0.414$, $p=0.327$; n=11)

and the lemurids (PCA 1: $K=0.430$, $p=0.207$ and PCA 2: $K=0.346$, $p=0.431$; n=14). Both the lepilemurids (n=6) and indriids (n=11) displayed high K values for niche axis one ($K=0.825$ and $K=0.934$), yet these values were statistically significant for the indriids only ($p=0.428$ and $p=0.031$, respectively). Both families exhibited no significant phylogenetic signal in the temperature niche axis ($K=0.507$, $p=0.415$ and $K=0.436$, $p=0.304$, respectively). It is important to keep in mind that samples sizes at the family level were relatively small, resulting in lower statistical power compared to using the total dataset.

Discussion

Previous studies have suggested that a lack of phylogenetic signal in ecological data is typical of island faunas [10,11,12,13], given that insular settings are well known for their adaptive radiations [21]. Our results from the climatic niche analysis of Malagasy primates are congruent with these findings and are among the first to demonstrate this pattern in island-restricted mammals. Analyses including all species revealed no correlation between phylogenetic relatedness and similarity in climatic niche. However, significant phylogenetic signal was detected at the family level for one group, the indriids. Phylogenetic signal within indriids could be the result of neutral (i.e. random) climatic niche evolution within this family, given that the K value was nearly 1, which is the

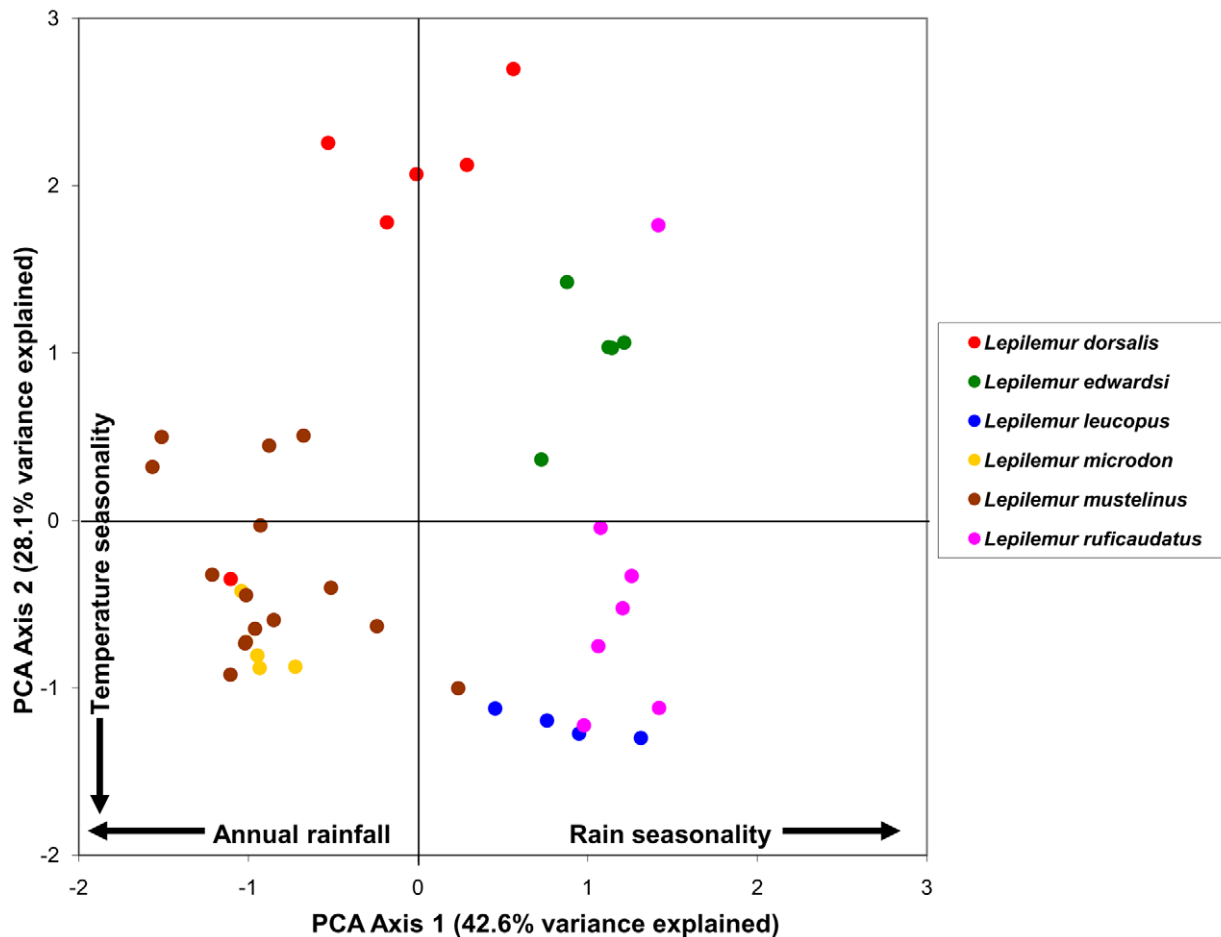


Figure 2. Plot of PCA scores representing the multivariate climatic niche space of Lepilemuridae species based on their known localities. The plot illustrates the same multivariate space as figures 1, 3–5. doi:10.1371/journal.pone.0011073.g002

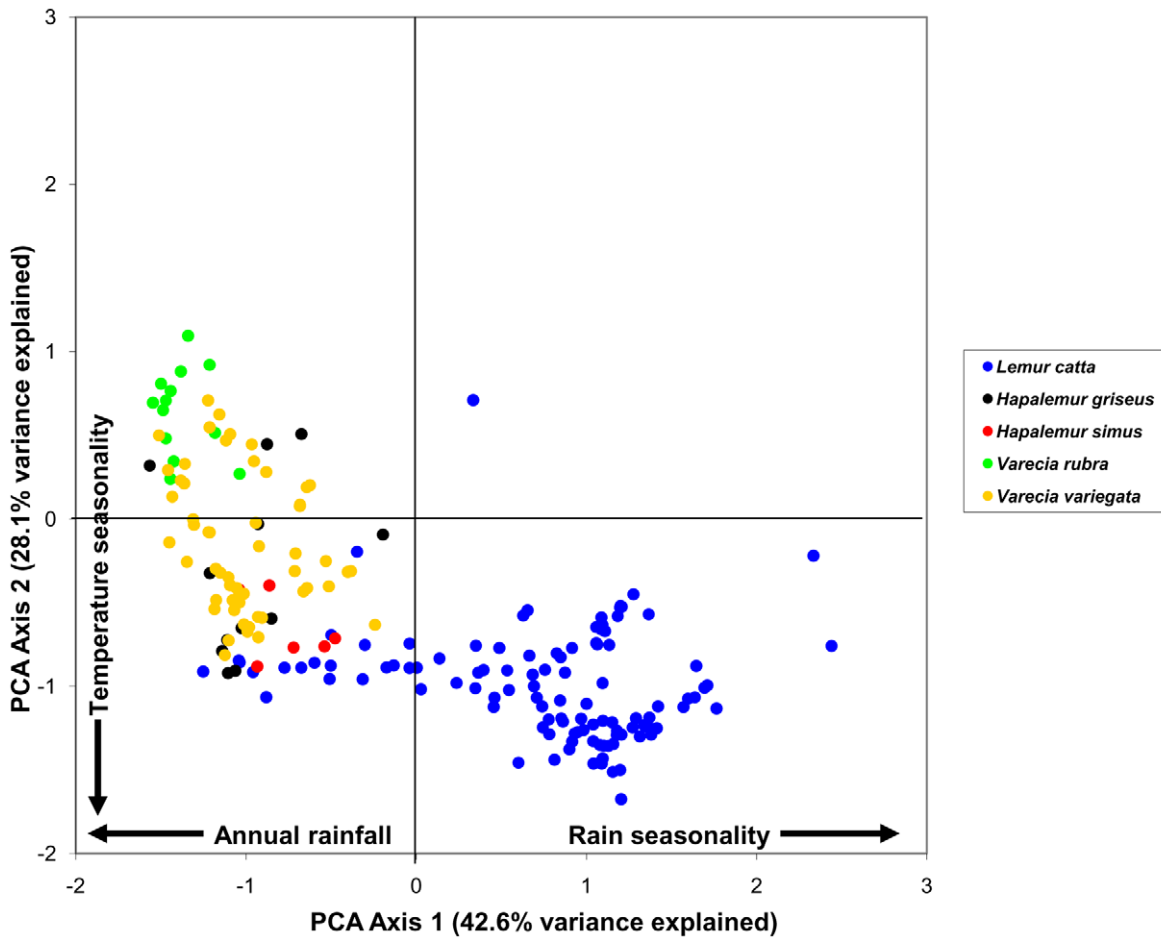


Figure 3. Plot of PCA scores representing the multivariate climatic niche space of Lemuridae (excluding *Eulemur*) species based on their known localities. The plot illustrates the same multivariate space as figures 1–2, 4–5. doi:10.1371/journal.pone.0011073.g003

degree of correlation between trait divergence and phylogenetic distance that is expected under Brownian motion. Alternatively, this result could relate to recent taxonomic revisions of the genus *Propithecus*, in which several subspecies were elevated to specific status [22]. The division of a single widespread species into multiple allopatric species (as would result from taxonomic inflation [23]) may “artificially” increase phylogenetic signal, by reflecting patterns of geographic variation [1]. A future test of alternative taxonomic hypotheses is possible using an ecological niche modeling approach [24].

A closer look at patterns of environmental tolerance among Malagasy primates reveals interesting evolutionary relationships. Although some sister species differ little in their climatic niche (e.g., *Varecia rubra* and *V. variegata* for rainfall tolerances; *Propithecus deckeni* and *P. coronatus* for temperature tolerances), in several cases sister taxa are markedly dissimilar (e.g., *Cheirogaleus medius* and *C. major* for rainfall tolerances; *Lepilemur microdon* and *Lepilemur edwardsi* for temperature tolerances). Furthermore, some distantly related species are more similar in their climatic niche (e.g., *Indri indri* and *Varecia variegata* for rainfall and temperature tolerances) than closely related species. Such similarities between less-related species could be the result of two different evolutionary processes. Non-sister species with similar climatic niches may have retained the ancestral niche through time, and therefore be more similar than expected based on their phylogenetic relatedness

[e.g., phylogenetic niche conservatism, sensu 1]. Alternatively, non-sister species might have independently derived the same niche through convergent evolution. Unlike many previous ecological niche modeling studies [25,26], we did not use phylogenetic methods to infer the niche of hypothetical ancestral taxa because of the low precision of ancestral reconstructions [27,28,29,30]. As a consequence, we are less able to make statements about the direction in which niche evolution occurred.

Nonetheless, visualizing the niche space of lemurs provides a view of the distribution of each species in relation to climatic, and thus habitat, parameters. For example, the ecological space occupied by the genus *Eulemur* is nearly equivalent to the space occupied by all the Malagasy primates included in our analysis (Fig. 4). However, within the genus *Eulemur*, species vary in total niche space occupied. *Eulemur rufus*, a broadly-distributed species that occurs in both the seasonal dry deciduous forests of the west and humid rainforests of the east, has very large niche breadth. In contrast, *Eulemur sanfordi*, which is restricted to the rainforests of northeastern Madagascar, is much more limited in terms of total niche space. Furthermore, an interesting situation occurs between the sister taxa *E. fulvus*, and the group including *E. collaris* and *E. albocollaris*, in which localities containing the latter group fall within the *E. fulvus* ecospace. We interpret this to indicate that the climatic niches of *E. collaris* and *E. albocollaris* are more specialized than, and are nested within, the *E. fulvus* niche. Without inferring

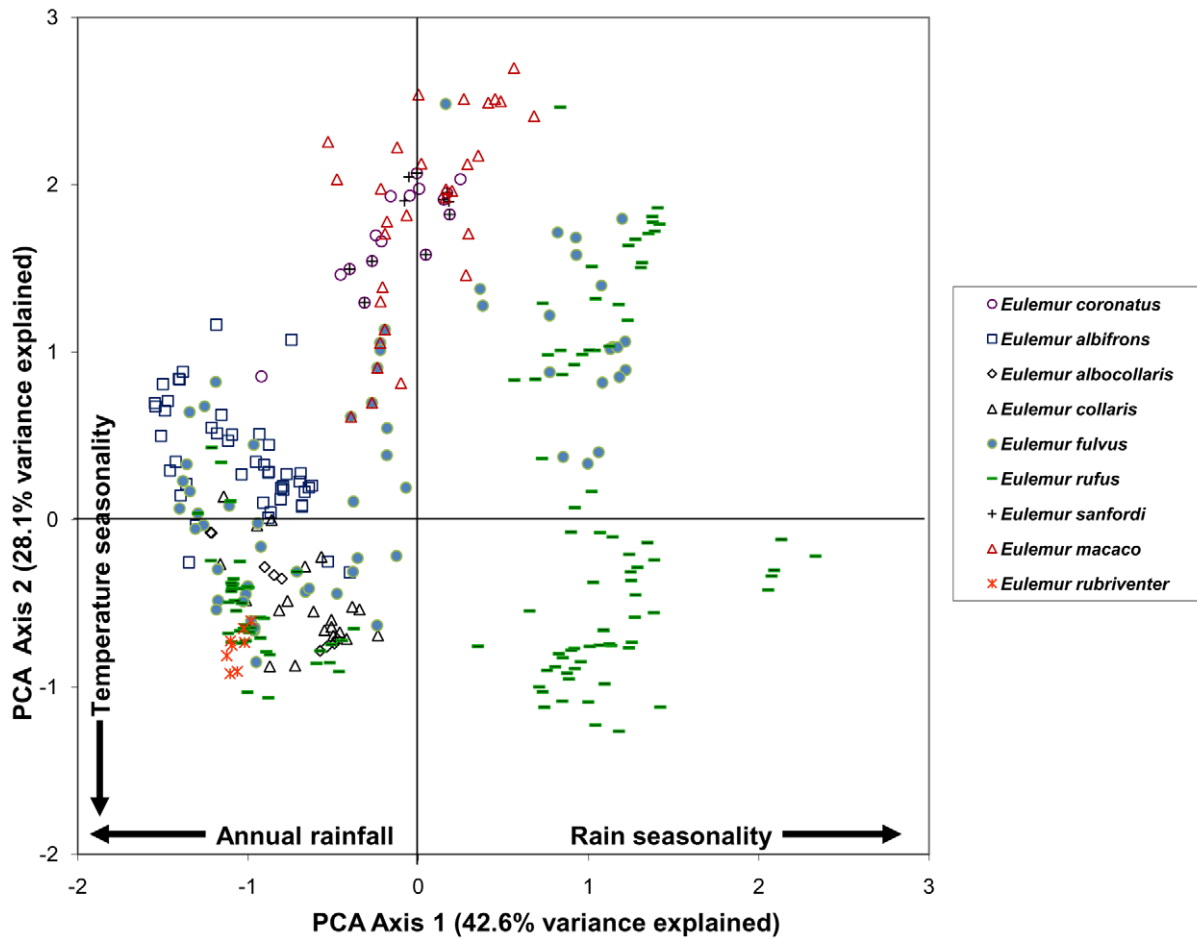


Figure 4. Plot of PCA scores representing the multivariate climatic niche space of *Eulemur* species based on their known localities. The plot illustrates the same multivariate space as figures 1–3, 5. doi:10.1371/journal.pone.0011073.g004

ancestral niches, the direction in which this evolutionary change occurred is difficult to discern. The sister taxa to the *E. fulvus* – *E. collaris* – *E. albocollaris* group is *E. rufus*, a species with a broad niche similar to that of *E. fulvus*. However, the sister taxa to this species group (*E. albifrons* and *E. sanfordi*), have comparatively narrow niches.

As has been previously demonstrated for both the recently extinct giant lemurs and still-extant Malagasy primates [31,32], our results demonstrate that all families and most genera are widely distributed across the island, with allopatric species that occupy a wide variety of habitats and climatic conditions. In fact, closely-related species occur sympatrically at only a few localities (e.g., *Eulemur mongoz* – *E. fulvus* at Ampijoroa; *E. coronatus* – *Eulemur sanfordi* at Ankarana; *E. rubriventer* – *E. fulvus* at Ranomafana). This phenomenon, in which closely related species tend not to occur sympatrically, is unique to the Malagasy primates, where the average phylogenetic distance among species in communities is relatively high compared to primate communities in other regions [33]. In contrast, distantly related Malagasy primate species often converge on a similar climatic niche space (Figs. 6–7). This can be seen in species pairs such as *Propithecus verreauxi* and *Microcebus griseorufus*, which are not closely related, but have a similar geographic distribution.

Our results have important implications for studies of the evolution of community structure in a phylogenetic context.

Ecologists have long hypothesized that closely related species have the strongest interspecific interactions. However, in the scenario of adaptive radiation, species may diverge from near relatives such that they interact just as strongly with less related species [21]. Consequently, ecological interactions among distantly related species play an important role in structuring local communities, as has been shown for *Anolis* lizards in Cuba [12].

Investigating the role that adaptation to different climatic niches has played in lemur evolution will contribute greatly to understanding this species-rich clade. However, there are limitations to our interpretations. First, climatic variables capture only one axis of a species overall niche space. Our estimates of niche overlap therefore may not represent cases of true sympatry at the within-site level. An important component of lemur community ecology and evolution is partitioning of habitats within a site [34,35,36,37,38]. An analysis of additional niche metrics such as diet, activity budget, and vertical habitat use may yield a finer-scale resolution of local distributions. Unfortunately, quantitative data for these variables are unavailable for most localities in our dataset. Second, current species distributions may be a result of recent dispersal, allopatric speciation or local extinction, and not a consequence of distributions actually tracking climatic conditions. Kamilar [39] found that geography (as a proxy for historical processes, such as dispersal) predicted primate species distributions independent of climatic conditions in Madagascar, although environmental factors

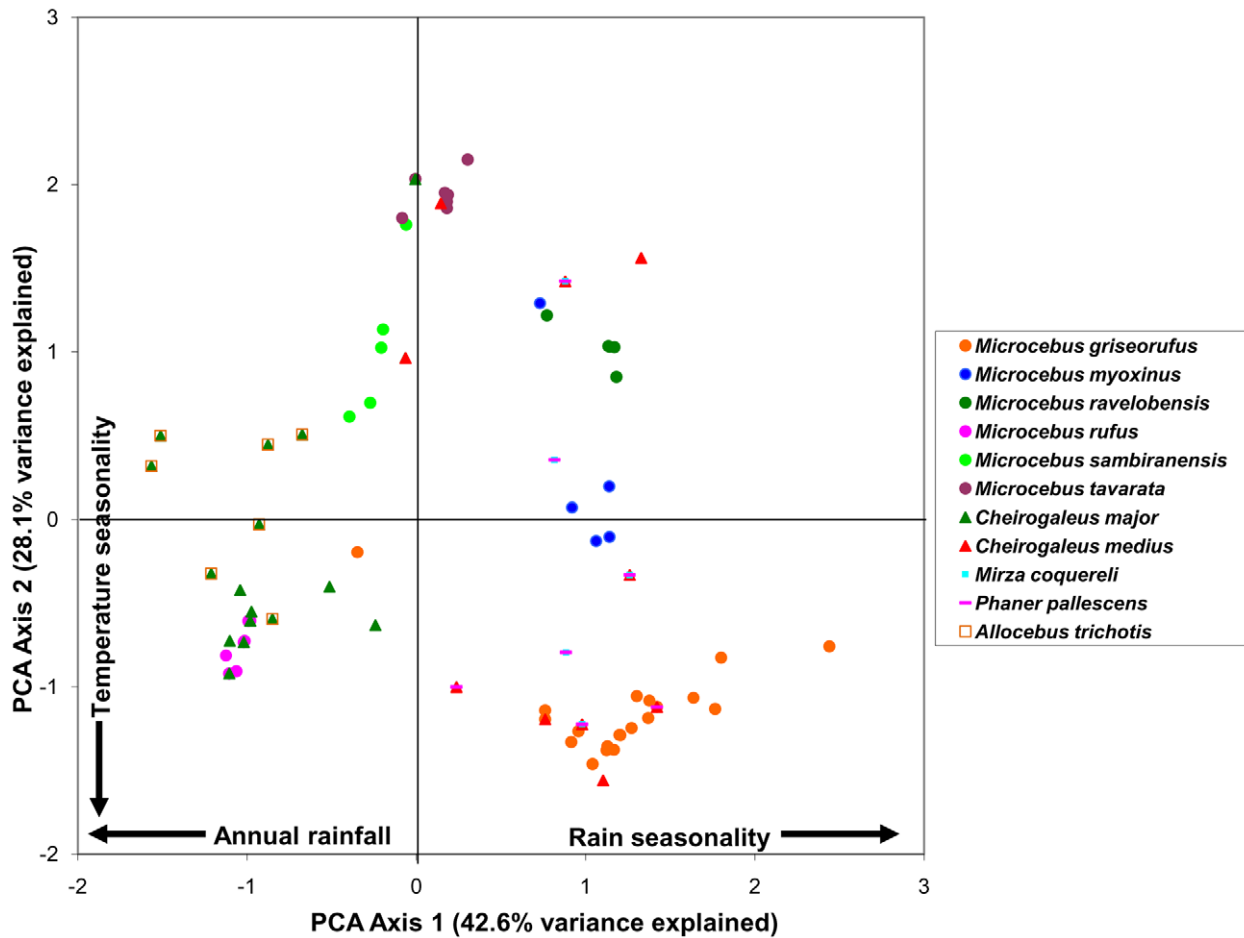


Figure 5. Plot of PCA scores representing the multivariate climatic niche space of Cheirogaleidae species based on their known localities. The plot illustrates the same multivariate space as figures 1–4. doi:10.1371/journal.pone.0011073.g005

explained even more variation in lemur community structure independent of geography. Likewise, Muldoon and Goodman [40] found a correlation between Malagasy non-volant mammal community structure and habitat type, suggesting that species ranges have been sorted along environmental gradients. Wilmé et al. [41] hypothesized that allopatric speciation at low altitudes during Quaternary climatic fluctuations explains the distribution of Madagascar’s extant diurnal lemurs, although this process may be more complex than initially thought [42].

Paleontological evidence demonstrates that at least 17 species of large-bodied lemurs have become extinct in the past few thousand years [43,44], resulting in a significant loss of both taxonomic and niche breadth in modern primate communities [31,45]. The extinct lemurs belonged to five families that comprise clades within extant Lemuriformes [46] and were distributed across Madagascar in several habitats [31,32]. Paleoenvironmental data is not available for most subfossil localities, and therefore their inclusion in this analysis is not currently possible. Furthermore, range contractions in some still-extant Malagasy primates have been extensive since the Pleistocene [32,47,48], presenting a problem for the interpretation sister species that appear to diverge in niche characteristics today. This scenario, for example, is displayed by two species pairs in our data set (e.g., *Lepilemur leucopus* and *L. ruficaudatus*; *Hapalemur griseus* and *Prolemur simus*). However, phylogenetic studies of Malagasy primates demonstrate a tendency

for sister species to be found in parapatry [49], suggesting that current lemur distribution patterns maintain a signal that at least partly reflects the original geography of speciation [42].

Third, because of small sample sizes for family-level comparisons, and given the current instability of lemur taxonomy [23,50,51,52], more data are needed to confirm and explore this pattern. Taxon sampling has been shown to affect the performance of statistical tests of trait associations [53]. Despite these caveats, we believe our results are sufficiently robust to suggest a lack of phylogenetic signal in the climatic niche of Malagasy lemurs.

We have demonstrated a pattern of niche divergence among closely related species of Malagasy primates, as has been found in other taxa [12,13,25,26]. It thus appears that phylogenetic signal should not necessarily be the expected outcome of evolutionary diversification [1]. Our results further suggest that climatic diversity plays a key role in generating primate diversity in Madagascar. Key areas in each of the island’s climatic regimes must be built into future protected areas Madagascar’s exceptional biological diversity is to be preserved [54].

Materials and Methods

Data Collection

We collected data from a total of 43 lemur species, comprising 1064 site by species samples (File S1). We follow the taxonomy of

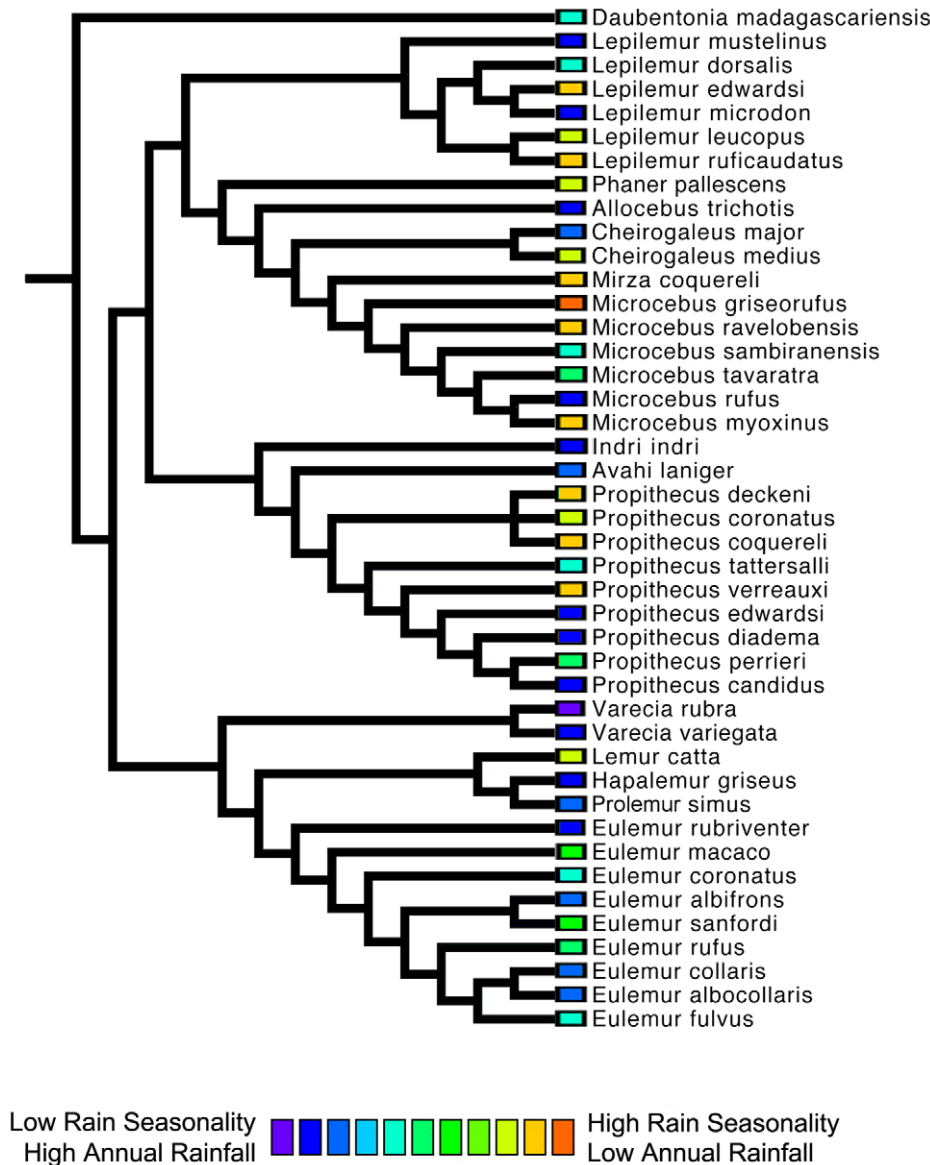


Figure 6. A phylogenetic perspective of Malagasy primate niche space as defined by rainfall variables (principal component 1). There is a no significant phylogenetic signal in this niche axis for all species comparisons ($p=0.116$), or within the *Lepilemuridae* ($p=0.428$), *Cheirogaleidae* ($p=0.265$), or *Lemuridae* ($p=0.207$) families. The *Indriidae* display the highest level of phylogenetic signal in the rainfall niche axis ($p=0.031$). Also note that several distantly related species converge on a similar niche space. doi:10.1371/journal.pone.0011073.g006

Mittermeier et al. (2006). Only species with at least five known localities were included in the study. We obtained the majority of locality data from Wilmé et al. [41]. This dataset was supplemented with published and unpublished data provided by the KMM and field researchers. These datasets contained the latitude and longitude of each site to the 0.01 degree. We followed previous ecological modeling studies by characterizing climatic niche space based on the abiotic conditions that each species is known to tolerate [24,39,55]. Species niche spaces are therefore based on the climatic conditions as defined by their known occurrences. Because our dataset is not exhaustive, this measurement represents the minimum known environmental niche space of a species. Because climate is a widely used proxy for habitat in comparative studies [39,56,57,58], the climatic niche space can be viewed as broadly representing the habitat niche space for each species.

We obtained the abiotic variables from the WorldClim GIS climate database [59]. This database contains 19 climate and one topographic variable (altitude) at a ~ 1 km resolution. The climate variables include various measures of rainfall and temperature patterns, including mean and extreme annual values. The WorldClim database is created by interpolating weather data gathered during the past 50+ years from over 100 weather stations distributed throughout Madagascar. We used the “extract to point” function in ArcGIS to obtain the climate data for each locality.

Our phylogeny was based on three sources: Mayor et al. [22] for *Propithecus*, Yoder and Heckman [60] for *Microcebus*, and Horvath et al. [61] for the remaining taxa, as well as the tree topology above the species level. We utilized equal branch lengths (i.e. branch lengths set to 1.0) instead of the absolute estimated

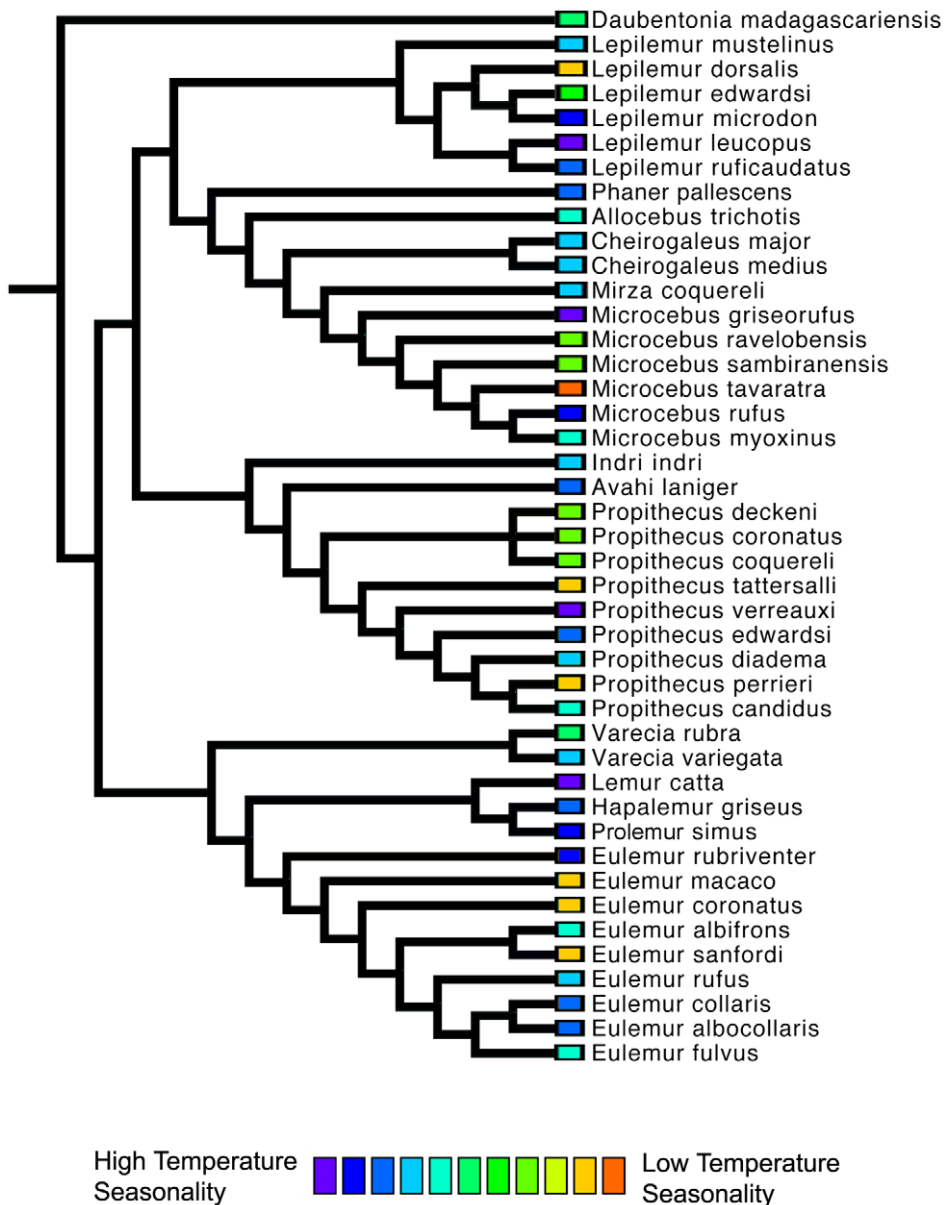


Figure 7. A phylogenetic perspective of Malagasy primate niche space as defined by temperature variables (principal component 2). There is no significant phylogenetic signal in this niche axis for all species comparisons ($p=0.568$), or within families (Lepilemuridae ($p=0.415$), Cheirogaleidae ($p=0.327$), Indriidae ($p=0.304$), Lemuridae ($p=0.431$)). Also note that several distantly related species converge on a similar niche space.
doi:10.1371/journal.pone.0011073.g007

divergence times between species. This procedure is unlikely to have a large impact on the results due to the fact that the PHYSIG analysis uses a randomization approach (consequently the magnitudes of branch lengths are less important), but was needed because well-established divergence times were unavailable for numerous species.

Data Analyses

We conducted a principal components analysis (PCA) to quantify lemur niches in multidimensional space. This allows us to account for covariation among variables and reduces the dimensionality of our dataset [62]. Before we conducted the PCA, we constructed a covariation matrix among all variables. Examining the covariation matrix allowed us to minimize the

degree of multicollinearity in our dataset by removing variables that displayed r^2 values greater than 0.85. Although a PCA accounts for covariation among variables, including several variables that are highly correlated can produce spurious results [62]. Using this criterion, we removed 11 variables from our initial dataset. Therefore, our PCA included the following nine variables: 1) annual mean temperature, 2) isothermality ((mean diurnal temperature range/temperature annual range)*100), 3) temperature seasonality (standard deviation*100), 4) temperature annual range (maximum temperature of warmest month-minimum temperature of coldest month), 5) annual precipitation, 6) precipitation during driest month, 7) precipitation seasonality (coefficient of variation of monthly rainfall), 8) precipitation during warmest quarter, and 9) altitude. We \log_{10} transformed the

variables before being entered into the PCA because the analysis is based on a parametric (e.g. Pearson's) correlation matrix [62]. We produced nine principal components to be certain that we accounted for all of the variation in our original dataset and that all of our components are orthogonal to each other [62].

To visualize niche space in an evolutionary context, we calculated each species mean PCA score for each component, and then plotted these values on a phylogenetic tree using Mesquite [63]. We calculated the degree of phylogenetic signal in niche space by using the K statistic presented by Blomberg et al. [14]. This statistic uses a generalized least squares approach to quantify the degree to which closely related species exhibit similar biological characteristics based on the topology and branch lengths of their phylogeny. The K statistic is a standardized ratio of the phylogenetic covariance of the species data to the expected covariance produced from Brownian motion. Because K is a standardized unit, K values based on different tree topologies and branch lengths can be compared. A K value of one indicates that the species trait is perfectly correlated to the phylogeny as expected under Brownian motion. Values less than one suggest that closely related species resemble each other less than expected, and values greater than one indicate that related species are more similar to each other than expected under Brownian motion [1,9,14]. To test for statistical significance, we used 9999 simulations to compare the K statistic generated from the real data to a distribution of randomized values. We calculated the K statistic with the Matlab script, PHYSIG.M, available from Ted Garland (UC Riverside). We measured phylogenetic signal for the first two niche axes (i.e.

principal components), as these accounted for more than 70% of the variation in the original data. To account for potential differences among the major Malagasy primate clades, we examined the degree of phylogenetic signal in all Malagasy primates, as well as the lepilemurids, cheirogaleids, indriids, and lemurids separately. The one drawback of examining phylogenetic signal at the family level is the smaller number of species in these taxonomic units. Blomberg et al. [14] showed that statistical power declines with sample sizes less than 20. Therefore, some caution should be used when interpreting statistically non-significant results for these analyses because Type II error rates are higher.

Supporting Information

File S1 Data used in the analyses.

Found at: doi:10.1371/journal.pone.0011073.s001 (0.12 MB PDF)

Acknowledgments

We thank Shawn Lehman for providing unpublished locality data. Seth Dobson, Charlie Nunn, Chris Gilbert, Andrea Baden, and two anonymous reviewers provided helpful comments that improved an earlier version of the manuscript.

Author Contributions

Conceived and designed the experiments: JMK KMM. Analyzed the data: JMK. Wrote the paper: JMK KMM.

References

- Losos JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11: 995–1007.
- Wiens JJ, Graham CH (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics* 36: 519–539.
- Anderson MT, Lachance M-A, Starmer WT (2004) The relationship of phylogeny to community structure: the cactus yeast community. *American Naturalist* 164: 709–721.
- Fleagle JG, Reed KE (1999) Phylogenetic and temporal perspectives on primate ecology. In: Fleagle JG, Janson C, Reed KE, eds. *Primate Communities*. New York: Cambridge University Press. pp 92–115.
- Johnson MTJ, Stinchcombe JR (2007) An emerging synthesis between community ecology and evolutionary biology. *Trends in Ecology & Evolution* 22: 250–257.
- Swenson NG, Enquist BJ, Pither J, Thompson J, Zimmerman JK (2006) The problem and promise of scale dependency in community phylogenetics. *Ecology* 87: 2418–2424.
- Chazdon RL, Careaga S, Webb C, Vargas O (2003) Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol Monogr* 73: 331–348.
- Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in Hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist* 168: 579–596.
- Revell LJ, Harmon LJ, Collar DC (2008) Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 57: 591–601.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33: 475–505.
- Edwards EJ, Donoghue MJ (2006) *Pereskia* and the origin of the cactus life form. *Am Nat* 167: 777–793.
- Losos JB, Leal M, Glor RE, Queiroz Kd, Hertz PE, et al. (2003) Niche lability in the evolution of a Caribbean lizard community. *Nature* 423: 542–545.
- Knouft JH, Losos JB, Glor RE, Kolbe JJ (2006) Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology Letters* 8: S29–S38.
- Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57: 717–745.
- Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R (1996) Ancient single origin for Malagasy primates. *Proceedings of the National Academy of Sciences, USA* 93: 5122–5126.
- Yoder AD, Yang ZH (2004) Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. *Molecular Ecology* 13: 757–773.
- Jury M (2003) The climate of Madagascar. In: Goodman S, Benstead J, eds. *The Natural History of Madagascar*. Chicago: The University of Chicago Press. pp 75–85.
- Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends Ecol Evol* 19: 497–503.
- Jernvall J, Wright PC (1998) Diversity components of impending primate extinctions. *Proc Natl Acad Sci USA* 95: 11279–11283.
- Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, et al. (2006) *Lemurs of Madagascar*. Washington D.C.: Conservation International.
- Schluter D (2000) *The Ecology of Adaptive Radiation*. New York: Oxford University Press.
- Mayor MI, Sommer JA, Houck ML, Zaonarivelo JR, Wright PC, et al. (2004) Specific status of *Propithecus* spp. *International Journal of Primatology* 25: 875–900.
- Tattersall I (2007) Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evolutionary Anthropology* 16: 12–23.
- Raxworthy CJ, Ingram CM, Rabibisoa N, Pearson RG (2007) Applications of ecological niche modeling for species delimitation: A review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. *Syst Biol* 56: 907–923.
- Rice NH, Martinez-Meyer E, Peterson AT (2003) Ecological niche differentiation in the *Aphelocoma* jays: a phylogenetic perspective. *Biol J Linn Soc* 80: 369–383.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* 58: 1781–1793.
- Schluter D, Price T, Moers AO, Ludwig D (1997) Likelihood of ancestor states in adaptive radiation. *Evolution* 51: 1699–1711.
- Webster AJ, Purvis A (2002) Testing the accuracy of methods for reconstructing ancestral states of continuous characters. *Proc R Soc Lond Ser B-Biol Sci* 269: 143–149.
- Martins EP (1999) Estimation of ancestral states of continuous characters: A computer simulation study. *Syst Biol* 48: 642–650.
- Losos JB (1999) Commentaries - Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Anim Behav* 58: 1319–1324.
- Godfrey LR, Jungers WL, Reed KE, Simons EL, Chatrath PS (1997) Subfossil lemurs. Inferences about past and present primate communities in Madagascar. In: Goodman SM, Patterson BD, eds. *Natural Change and Human Impact in Madagascar*. Washington: Smithsonian Institution Press. pp 218–256.
- Muldoon KM, Godfrey LR, Jungers WL (2009) Geographic patterning in subfossil primate community dynamics in Madagascar. *American Journal of Physical Anthropology* S44: 270.

33. Kamilar JM, Guidi LM (2010) The phylogenetic structure of primate communities: Variation within and across continents. *Journal of Biogeography* 37: 801–813.
34. Hladik CM, Charles-Dominique P, Petter JJ (1980) Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pariente EPG, et al. (1980) *Nocturnal Malagasy Primates*. New York: Academic Press. pp 41–74.
35. Schreier BM, Harcourt AH, Coppeto SA, Somi MF (2009) Interspecific competition and niche separation in primates: A global analysis. *Biotropica* 41: 283–291.
36. Dammhahn M, Kappeler PM (2008) Small-scale coexistence of two mouse lemur species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive environment. *Oecologia* 157: 473–483.
37. Ganzhorn JU (1997) Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. *Journal of Zoology (London)* 241: 533–542.
38. Ganzhorn J (1989) Niche separation of seven lemur species in eastern rainforest of Madagascar. *Oecologia* 79: 279–286.
39. Kamilar JM (2009) Environmental and geographic correlates of the taxonomic structure of primate communities. *American Journal of Physical Anthropology* 139: 382–393.
40. Muldoon KM, Goodman SM (2010) Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *Journal of Biogeography* 37: 1144–1159.
41. Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar's microendemic biota. *Science* 312: 1063–1065.
42. Pearson RG, Raxworthy CJ (2009) The evolution of local endemism in Madagascar: Watershed versus climatic gradient hypothesis evaluated by null biogeographic models. *Evolution* 63: 959–967.
43. Godfrey LR, Jungers WL (2003) Subfossil lemurs. In: Benstead SMG, ed. *The Natural History of Madagascar*. Chicago: The University of Chicago Press. pp 1247–1252.
44. Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, et al. (2004) A chronology for late prehistoric Madagascar. *Journal of Human Evolution* 47: 25–63.
45. Fleagle JG, Reed KE (1996) Comparing primate communities: a multivariate approach. *Journal of Human Evolution* 30: 489–510.
46. Orlando L, Calvignac S, Schebelen C, Douady CJ, Godfrey LR, et al. (2008) DNA from extinct giant lemurs links archaolemurids to extant indriids. *BMC Evolutionary Biology* 8: 121.
47. Godfrey LR, Simons EL, Jungers WL, DeBlieux DD, Chatrath PS (2004) New discovery of subfossil *Hapalemur simus*, the greater bamboo lemur, in western Madagascar. *Lemur News* 9: 9–10.
48. Muldoon KM, DeBlieux DD, Simons EL, Chatrath PS (2009) The subfossil occurrence and paleoecological significance of small mammals at Ankiliteo Cave, southwestern Madagascar. *Journal of Mammalogy* 90: 1111–1131.
49. Pastorini J, Thalmann U, Martin RD (2003) A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences USA* 100: 5879–5884.
50. Andriaholinirina N, Rabarivola C, Zaramody A, Roos C, Zinner D, et al. (2006) Cytogenetic and molecular characterization of the new described sportive lemur *Lepilemur jamesi* (Louis et al., 2006). *Primate Report* 74: 25–33.
51. Louis EE, Engberg SE, McGuire SM, McCormick MJ, Randriamampionona R, et al. (2008) Revision of the mouse lemurs, *Microcebus* (Primates, Lemuriformes), of northern and northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro Classified Forest. *Primate Conservation* 23: 19–38.
52. Andriantompohavana R, Lei R, Zaonarivelo JR, Engberg SE, Nalanirina G, et al. (2007) Molecular phylogeny and taxonomic revision of the woolly lemurs, genus *Avahi* (Primates: Lemuriformes). *Occasional Papers, Museum of Texas Tech University* 51: 1–59.
53. Ackerly DD (2000) Taxon sampling, correlated evolution, and independent contrasts. *Evolution* 54: 1480–1492.
54. Kremen C, Cameron A, Moilanen A, Phillips SJ, Thomas CD, et al. (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320: 222–225.
55. Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12: 2272–2281.
56. Ossi KM, Kamilar JM (2006) Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behavioral Ecology and Sociobiology* 61: 53–64.
57. Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
58. Chapman CA, Wrangham RW, Chapman IJ, Kennard DK, Zanne AE (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15: 189–211.
59. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
60. Yoder AD, Heckman KL (2006) Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. In: Lehman SM, Fleagle JG, eds. *Primate Biogeography*. New York: Springer. pp 255–268.
61. Horvath JE, Weisrock DW, Embry SL, Fiorentino I, Balhoff JP, et al. (2008) Development and application of a phylogenomic toolkit: Resolving the evolutionary history of Madagascar's lemurs. *Genome Research* 18: 489–499.
62. McGarigal K, Cushman S, Stafford S (2000) *Multivariate statistics for wildlife and ecology research*. New York: Springer.
63. Maddison WP, Maddison DR (2007) *Mesquite: A modular system for evolutionary analysis*. Version 2.0. <http://mesquiteproject.org>.