Summer 8-10-2017

The influence of phylogeny and niche differentiation on the diets of Malagasy primates

Rebekka S. Hughes
CUNY Hunter College

The influence of phylogeny and niche differentiation on the diets of Malagasy primates

by

Rebekka Hughes

Submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Anthropology, Hunter College
The City University of New York

2017

Thesis Sponsor:

August 10, 2017	Andrea Baden
Date	Signature

August 10, 2017	Christopher Gilbert
Date	Signature of Second Reader

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT:

The influence of phylogeny and niche differentiation on primate diet has not been well studied, especially in Malagasy communities. In general, studies of anthropoid diet have shown a correlation between similarity in diet and phylogeny, indicating that phylogeny has an effect on primate diet. This study tests the hypothesis that, like haplorhines, Malagasy primates will show a strong correlation between phylogeny (as measured by divergence distance) and dietary similarity. Phylogenetic and dietary data were obtained from the existing literature. Using Mantel tests, correlations between divergence distance and percent similarity in diet were shown for lemurs with sufficient data in each of four communities: Ranomafana National Park (n=9), Berenty Private Reserve (n=4), Kirindy Forest (n=5), and Beza Mahafaly Special Reserve (n=3). Results were mixed between the communities, showing both a strong negative correlation between divergence distance and overall dietary similarity for Ranomafana and no correlations for the other sites, using 0.05 as threshold of significance. Mixed results raise questions about factors influencing community composition in Madagascar. Strepsirrhines seem to differ from haplorhines in whether phylogeny or niche differentiation shows a stronger influence over diet; however, this may depend on the region in Madagascar. These results raise questions as to the differences in evolutionary processes across regions in Madagascar.

BACKGROUND:

Stepsirrhines and haplorhines differ in many ways including a smaller average group size for strepsirrhines as well as cathemerality, seasonal mating, lack of sexual dimorphism, and female dominance over males in many lemur groups (Wright 1999). In addition to the differences outlined previously, anthropoids tend to conform to the risk aversion hypothesis of growth, Malagasy primates do not (Godfrey et al. 2004). The risk aversion hypothesis maintains that by slowing growth and development, folivorous primates are able to reduce the risk of starvation in juveniles, whereas frugivorous primates reduce the risk of juvenile mortality by quickening growth and development. While folivorous anthropoids tend to have faster developmental courses than frugivorous anthropoids, folivorous lemurs have slower growth than more frugivorous lemurs (Godfrey et al. 2004). How can this change be seen through phylogeny? In what ways does environment affect dietary choices? How do phylogeny and environment together play a role in lemur feeding ecology?

The influence of phylogeny on the diets of primates has recently been investigated by Porter el al. (2014). Focusing on haplorhine primate communities across the Old and New World, the authors examined the relationship between divergence distance and dietary similarity in order to understand more about community composition, taxonomic ecology, and how species living in the same habitat interact with each other. Using the sites of Kuala Lompat (Krau Game Reserve, Malaysia), Cocha Cashu (Manu National Park, Peru), Raleighvallen-Voltsberg National Park (Suriname), Kibale Fores (Uganda), and Tai Forest (Ivory Coast), Porter et al. (2014) found significant results indicating that divergence distance and dietary similarity are related, meaning that primate pairs with more recent divergence dates tend to have more similar diets. Following

2

Porter et al. (2014), this study examines the relationship between diet and phylogeny in Malagasy strepsirrhine communities in order to gain a deeper understanding into Malagasy community ecology and composition.

As far back as Darwin, researchers have been interested in the causes of community assembly and competition. A staggering percentage of genera exist with only one species present in any given community (Elton 1946). Many different genera are able to live in the same community, while species within those genera generally do not cohabitate. This pattern of species distribution could be from undetected differences in the habitats or because of historical competition (Elton 1946). It has been argued that more closely related species are in greater competition, making coexistence less possible due to competitive exclusion (Cardillo et al. 2008). Similarly, according to Fox's rule of assembly, each species in a community should come from different genera when there is low resource richness (Fox 1987). As resource availability increases, so will species richness. The addition of species follows a pattern according to Fox's rule in which species can be added to a community based on a tier system, adding one species per genus as resources become more diversified (Fox 1987). This tier system is supported by Houle's (1997) finding that aggression between species is higher when they are phylogenetically more similar. Furthermore, behavior and ecology are easier to change than morphology and physiology (Fox 1987). Therefore, species with similar diets will have dissimilar microhabitats, even if they share similar macrohabitats. The opposite is also true; species with similar microhabitats will have dissimilar diets (Fox 1987). Kamilar and Ledogar (2011) show evidence of this rule in Malagasy primates.. It also seems to be exhibited that species co-occurrence in Malagasy primates has been affected by past competition, as it is shown through non-random structuring (Kamilar and Ledogar 2011).

Species assemblages can be clustered, overdispersed, or randomly dispersed, with a pattern of overdispersal being common on islands (Cardillo et al. 2008). Fitting with this general observation, Malagasy primate communities are considered overdispersed, meaning that primates communities in Madagascar are phylogenetically less closely related than expected by chance (Beaudrot and Marshall 2011). Ecological distance, as opposed to geographical distance for other primate communities, shows greater community similarity in Madagascar. Likewise, niche differentiation has a greater effect on Malagasy primates that dispersal limitation (Beaudrot and Marshall 2011). This suggests that niche differentiation is a predictor of Malagasy community composition; however, it is not compared to the effect of dietary similarity.

Community structure is influenced by community ecology, meaning that food competition may not be the primary factor in community structuring (Kamilar and Ledogar 2011). Current community structure occurs because of past competition and, therefore, current competition is not always the best indicator of the processes that create community structure (Kamilar and Ledogar 2011). However, phylogenetic divergence and ecological distance are positively correlated, making it less likely to have closely related species living together in Madagascar (Kamilar and Beaudrot 2013). This is possibly due to competitive exclusion (Kamilar and Beaudrot 2013).

Phylogenetic niche conservatism is another way of looking at community structure. Phylogenetic niche conservatism is the idea that there is a constraint which prevents niche expansion within populations (Pyron et al. 2015). Therefore, lineages maintain their ancestral ecology and overlap in both fundamental and realized niches. Species may vary more within a shared fundamental niche when they are closely related, resulting in different realized niches. This process is called niche constraint as opposed to conservatism. Furthermore, evolutionary

inertia and drift may affect phylogenetic niche conservatism more if selection does not have a strong influence on traits (Pyron et al. 2015). The processes of phylogenetic niche conservatism may also produce a pattern of divergent niches. This is often the result of niches being instantaneous. If a population experiences rapid change, divergence in niches may also happen more rapidly (Pyron et al. 2015).

Neutral theory asserts that community composition is shaped mainly by dispersal limitation as opposed to divergent niches (Beaudrot and Marshall 2011). In this instance dispersal limitation is a more powerful predictor of niche divergence than phylogeny. This suggests that geographical distance should be the best predictor of similarity of communities within a metacommunity. However, if similarity of communities is better predicted by ecological similarity, then niche processes are more likely acting upon community composition (Beaudrot and Marshall 2011).

Similar to Beaudrot and Marshall's (2011) hypotheses on community composition and as is shown for haplorhine primates in Porter et al. (2014), I predict that lemurs that have closer phylogenetic relationships will have more similar diets due to more similar morphology and adaptations. This would be shown through a significant negative relationship between divergence dates and percent similarity index of diet. If, however, lemur diets are more closely associated with niche differentiation, there should be no correlation between divergence dates and percent similarity index of diet.

As noted above with the case of the risk aversion hypothesis among others, strepsirrhines do not always follow the ecological patterns of haplorhines. This could be the case for diet, as lemurs have had to evolve life history adaptions in order to survive in Madagascar due to the high stochasticity seen on the island (Cowlishaw and Dunbar 2000; Dewar and Richard 2007;

Wright 1999). Due to this, it could be that niche differentiation is a stronger predictor of diet than phylogenetic distance. However, this view is now being challenged on the basis that the larger extinct lemurs have left larger seeds without a mode of dispersal, changing the Malagasy ecosystem (Dewar and Richard 2007). If this is the case, it is still probable that my hypothesis will hold true.

METHODS:

I targeted four sites in Madagascar for data collection from previously published studies. I only included sites had dietary data available for at least three sympatric primate species. Data were collected from published literature that had percentages of plant genera eaten by individual lemur species. If percentage data were unavailable, presence/absence data were substituted. Ideally all data would be from the same general time period and collected by as few people as necessary using the same methods for the collection of feeding data. Unfortunately, this was impossible to achieve, but consideration was taken to standardize data from the literature as much as possible. When data from multiple areas or times within a site were available, data from pristine forest areas during the wet season were used. Below are descriptions of the sites used in this paper (see Figure 1 and Table 1).

Ranomafana National Park

Ranomafana is in the rainforests of southeastern region of Madagascar at 21°16'S, 47°20'E (Wright et al. 2011; Figure 1). Rainfall follows a seasonal pattern, with the majority of rain falling in December through March. Plant species fruit at irregular intervals (Wright et al. 2011). Seven diurnal species (*Eulemur rufus, E. rubriventer, Hapalemur aureus, H. griseus, Prolemur*

simus, Propithecus edwasrsi, and *Varecia vaiegata*) and two nocturnal species (*Avahi laniger*

and *Microcebus rufus*) out of twelve possible species (75%) had percentage values of dietary

data that were able to be included in the analyses. *Cheirogaleus major* was also included in

analyses with presence/absence data. Two nocturnal species (*Daubentonia madagascariensis* and

Lepilemur microdon) did not have available dietary data (see Table 2).

Berenty Private Reserve

Berenty is located at 25°S, 46.3°E in a forest with both gallery forest areas and spiny forest areas

at the southeast tip of Madagascar (Droscher and Kappeler 2014; Figure 1). Seasonality here is

characterized by wet seasons during summer months and dry seasons during winter months.

Temperatures also range from hot during the wet season to cold during the dry season (Droscher

and Kappeler 2014). Two thirds of the six lemur species found a Berenty had sufficient dietary

data. *Eulemur rufus, Lemur catta,* and *Propithecus verreauxi* as well as *Lepilemur leucopus* had

percentage dietary data available. *Microcebus murinus* and *M. griseorufus* did not have the

necessary data (see Table 3).

Kirindy Forest

Kirindy (20°04'S, 44°40'E) is a seasonal forest on the central western coast of Madagascar (de

Winter et al. 2013; Figure 1). Seasonality is marked by a long dry season lasting from April until

November with a shorter wet season from December through March (de Winter et al. 2013). All

analyses at Kirindy were conducted from presence/absence data. Of eight lemur species, 62.5%

had sufficient available data. Diurnal *Eulemur rufus* and *Propithecus verreauxi* and nocturnal

Cheirogaleus medius, Microcebus berthae, and M. murinus were analyzed, leaving three

nocturnal species (*Lepilemur ruficaudatus, Mirza coquereli,* and *Phaner pallescens*) with

insufficient data (see Table 4).

Beza Mahafaly Special Reserve

Beza Mahafaly has both riverine and scrub forest and is located at 23°30'S, 44'E in southwestern

Madagascar (Gemmill and Gould 2008; Figure 1). The reserve has only a short wet season with a

long dry season (Crowley et al. 2014). Percentage data were available for 50% of lemur species

found at Beza Mahafaly (*Eulemur rufus and Lemur catta, but not Propithecus verreauxi, and for*

Microcebus griseorufus, but not M. rufus or Lepilemur leucopus) (see Table 5).

Data Analyses

Using divergence dates from Perelman et al. (2011), supplemented by Baab et al. (2014)

and Fausser et al. (2002), I used UPGMA clustering to create dendrograms in PAST 3.11

(Hammer et al. 2001). When species data were not available in these publications, data from the

genus level were used when appropriate. Dietary overlap was calculated using Schoener's Index

of Niche Overlap given as

$$PS = 1 - 0.5 \sum (|x_i - y_i|)$$

where PS is the percentage of diet that is similar, x_1 is the percentage of a plant genus eaten by

species x, and y_1 is the percentage of a plant genus eaten by species y. In this equation, a PS

value of zero means there is no dietary overlap, while a PS value of one indicates complete

dietary overlap. I used percentages when available for the top food resources. For all others, I

estimated percentages by equally distributing the percent remaining. If percentage data were

unavailable for a particular site, I used presence and absence of genera observed in the species'

diets. In these instances, a variation of Schoener's Index was conceptualized to be

$$PS = 1 - \frac{\sum(|x_i - y_i|)}{n}$$

where x_i and y_i are equal to 1 when a genus is present in the lemur diet and 0 when a genus is not

present, with n being the number of genera included in all lemur diets within the site. The PS

values and divergence distance found in each site used are summarized in Tables 6-9.

To analyze the data, I calculated a PS value for each species pair at a given site. I then

ran Mantel tests correlating divergence distance and PS values. Significance was set to P<0.05

level using 9999 permutations. These analyses were run in R3.3.2 using the ade4 package (R

Core Team 2016; Dray and Dufour 2007).

RESULTS:

Mantel test results indicate that there is no relationship between diet and phylogeny in the

majority of lemur communities in this study (see Figures 2-5 for scatterplots of the data).

Ranomafana National Park seems to be the exception with an *r* value of 0.5977 and $p \leq 0.002$.

For all other sites *r* values vary with $p \geq 0.3$. These numbers are summarized in Table 10.

Dendrograms for each site can be found in Figures 6-9.

DISCUSSION:

In total, my results did not reject the null hypothesis. While phylogenetic distance seemed

correlated with ecological distance at Ranomafana, there was no consistent correlation across

sites, with the other three sites having non-significant results, and thus there is no support for a

more general relationship between phylogenetic distance and ecological distance across

Madagascar. There could be many reasons for this. As has been shown with group size, sociocognitive skills, and lack of adherence to social theories, strepsirrhines do not always follow the pattern of haplorhines and it is highly possible that this would be the case for diet. When considering Cowlishaw and Dunbar (2000), lemurs have had to evolve adaptations in order to survive in a highly variable climate as is seen in Madagascar. Due to this, it could be that diet is more related to niche differentiation than phylogeny for Malagasy primates. Niche differentiation in diet would allow for lemurs to forage without as much competition from closely related species. Niche differentiation could also help explain the high percentage of nocturnal primate species found in Madagascar.

It could also be the case that the effects of phylogeny are being overshadowed by niche differentiation. Because evolution builds upon itself, behavior and anatomy in any taxon should be generally conserved while leaving room for species to develop ecological adaptations, with ecological and behavioral adaptations happening more readily (Fleagle and Reed 1996). Ecological niches are formed by variables in the environment, therefore it is conceivable that the same forces that are creating niches are also influencing adaptations in species. Species should adapt to their environment first by changing their ecology and behavior and then through morphology (Fleagle and Reed 1996). In this way, evolutionary forces are contributing to speciation through both phylogeny and niche differentiation both morphologically and behaviorally, respectively. It is possible that niche differentiation is a stronger factor than phylogeny in influencing diet. Although phylogeny, and thus morphology, may be a factor, it is slower to evolve than behavioral niche differentiation. While phylogenetic components would be seen with my analyses, niche differentiation would not be seen as readily.

Although these results contrast with those of Porter et al. (2014), they give us a greater

understanding of the differences between haplorhines and strepsirrhines. The results of this study add to a growing body of literature outlining the differences between the two groups which brings us closer to an understanding of anthropoid origins. What made us different? How did we evolve? These questions can only be answered by gathering comparative information on the ecology of both haplorhines and strepsirrhines. By comparing my results to that of Porter et al. (2014), we can see a glimpse of distinction between the evolutionary tracts taken by the different groups, with haplorhines showing a greater reliance on phylogenetic changes and strepsirrhines relying more on niche differentiation in order to live amongst one another in the same habitat.

Caveats

A major shortfall of my study is the small sample sizes at some of the sites, which could have drastically affected my results. The most robust sample size was found at Ranomafana, the only site to meet the set significance levels. By using more sites with higher proportions of species with percentage feeding data available, significance may be found more often. This would, however, require more comprehensive feeding studies at multiple sites in Madagascar. Additionally, there could be a difference between the sites used in this paper because Ranomafana also had the highest proportion of congeners that were able to be compared. Other sites that had congeners only had data for one of the species. In these cases, it is possible that results of the mantel test would greatly differ with the inclusion of feeding data for the non-sampled congener.

APPENDICES:

Figure 1. Map of sites used within this paper.

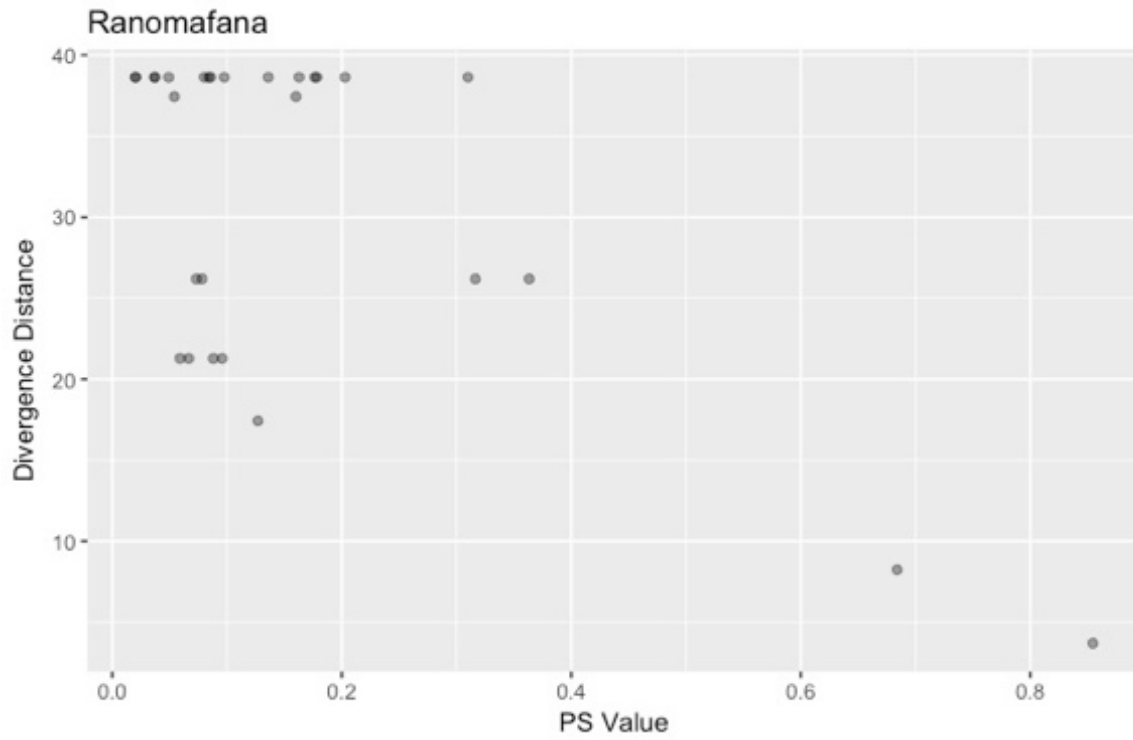Figure 2. Scatterplots of PS value against divergence dates at Ranomafana.
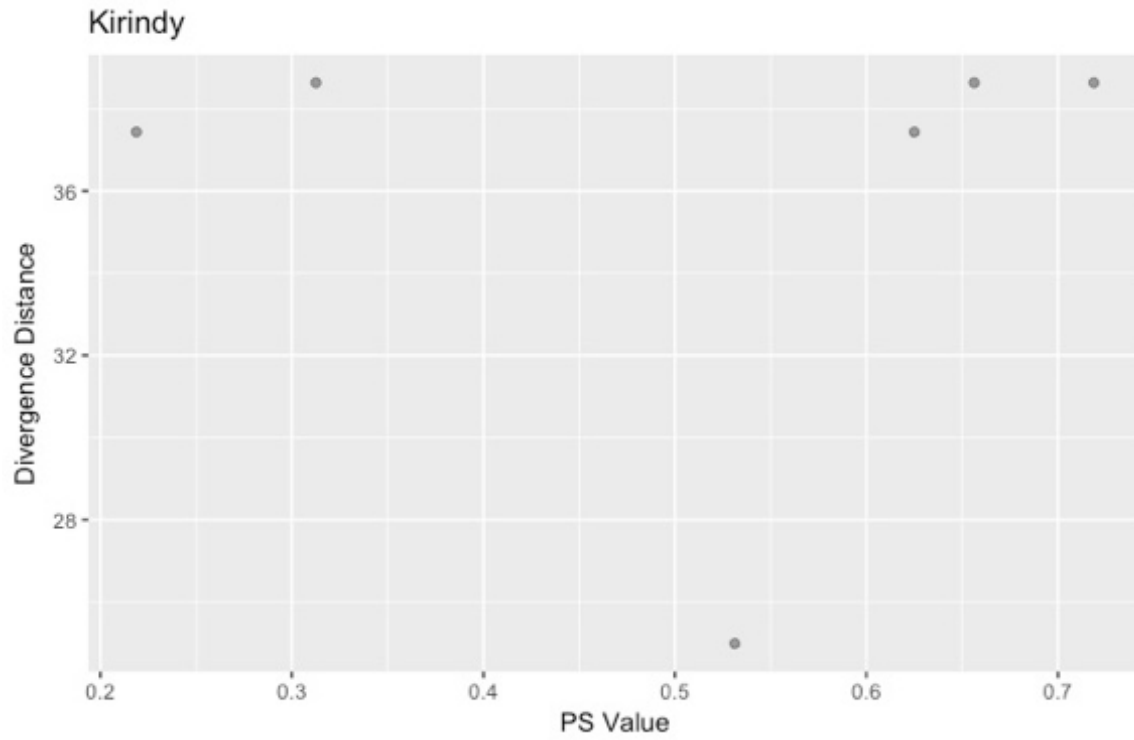
Figure 3. Scatterplots of PS value against divergence dates at Kirindy.
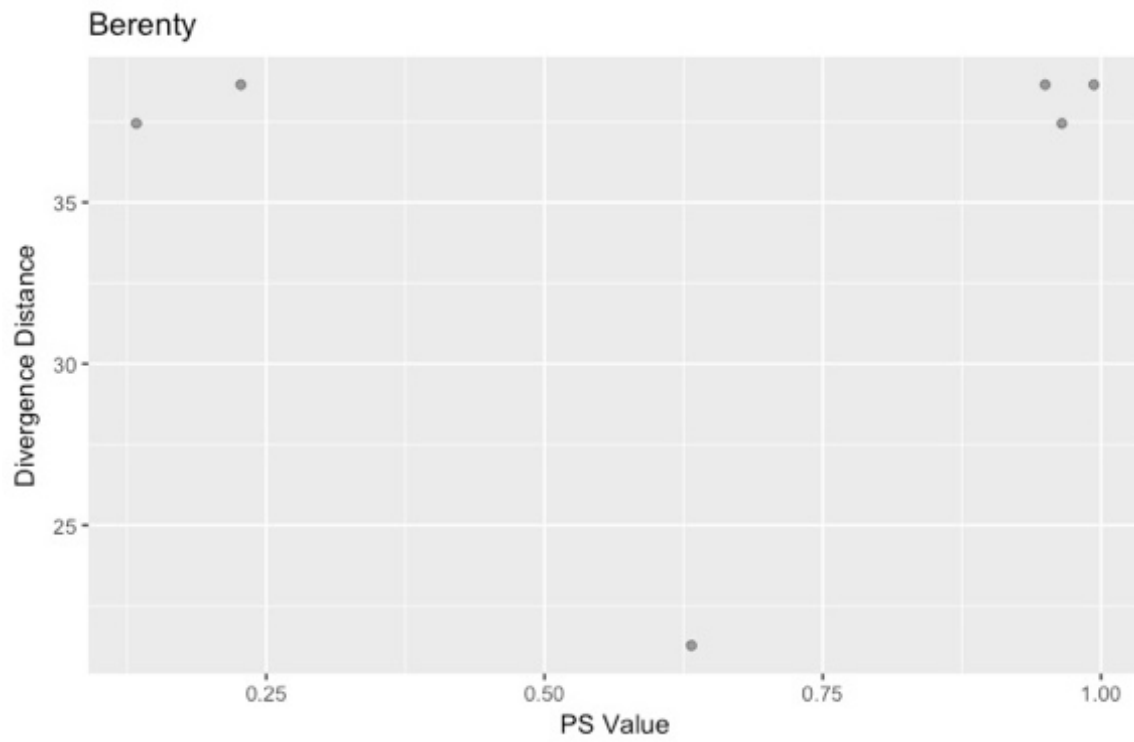
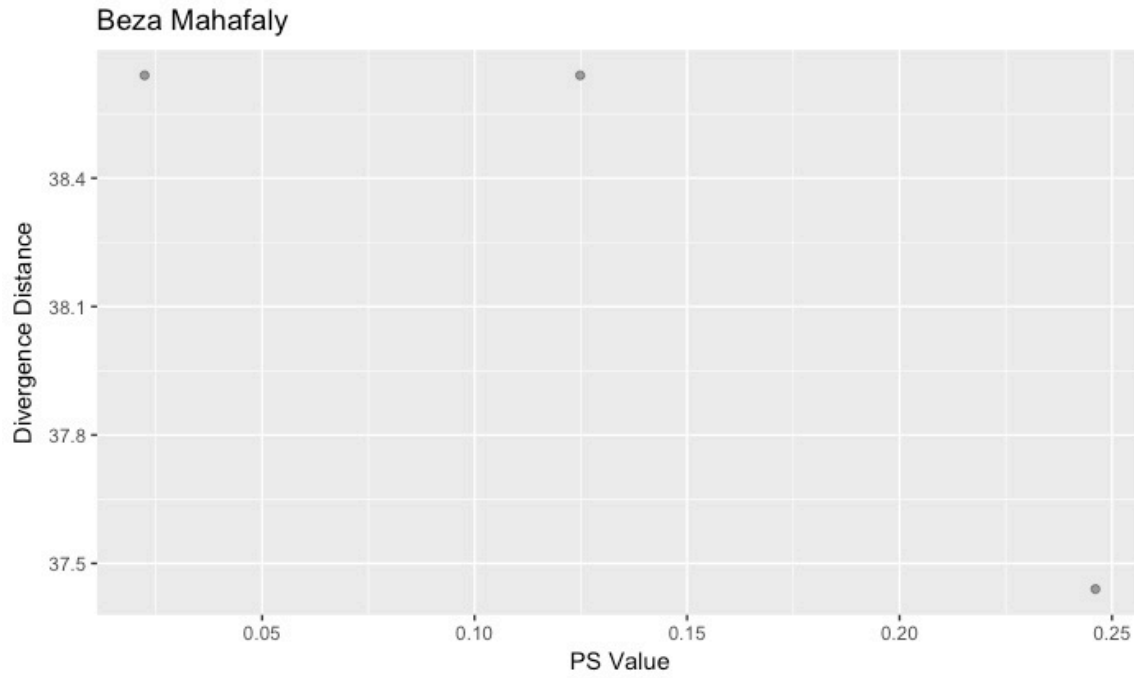Figure 4. Scatterplots of PS value against divergence dates at Berenty.

Figure 5. Scatterplots of PS value against divergence dates at Beza Mahafaly.
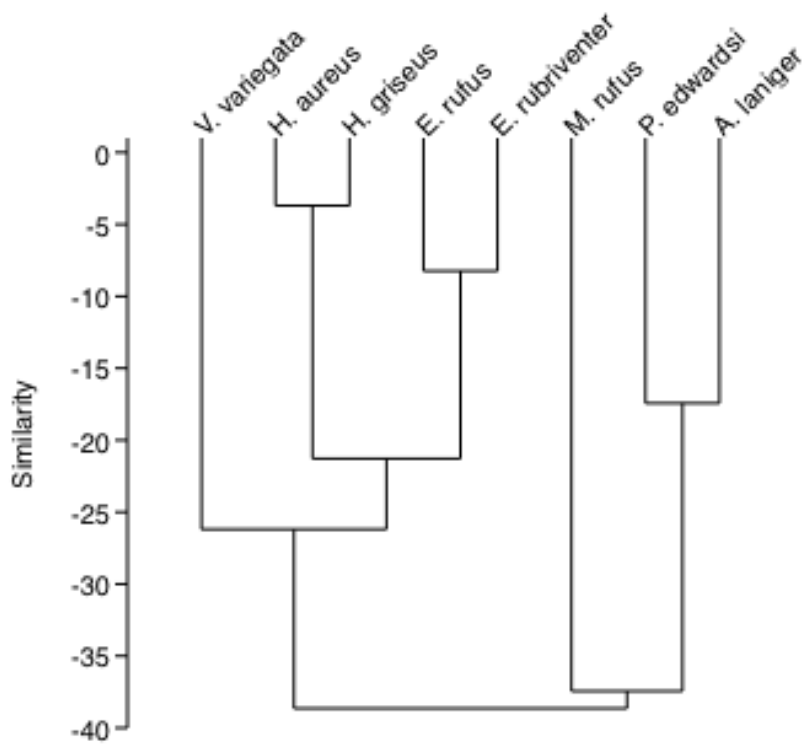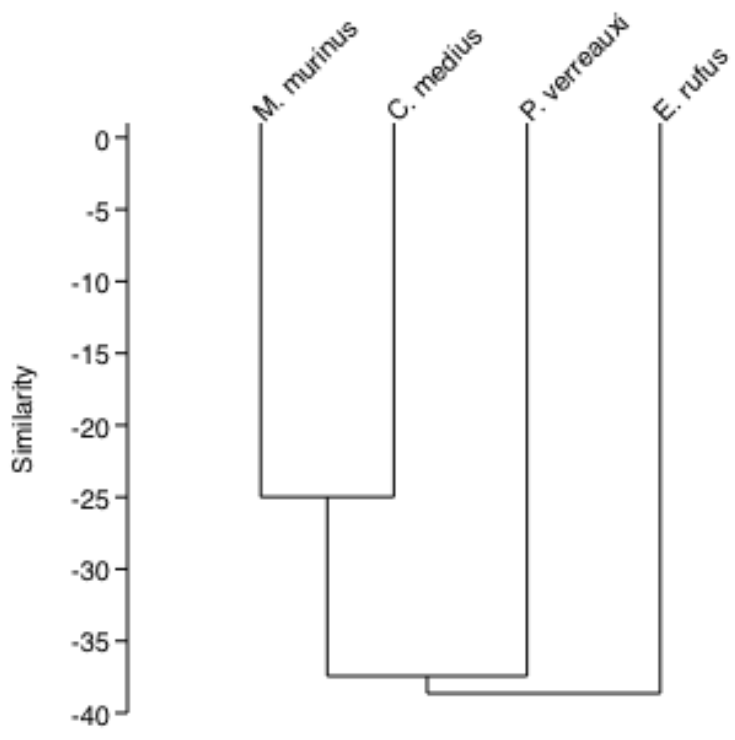
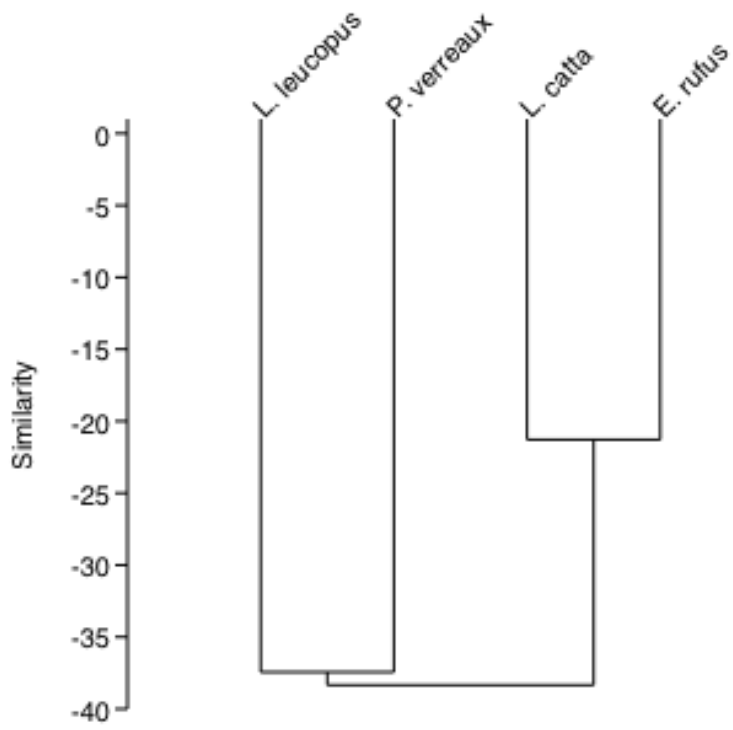Figure 6. Dendrogram for Ranomafana.

Figure 7. Dendrogram for Kirindy.

Figure 8. Dendrogram for Berenty.
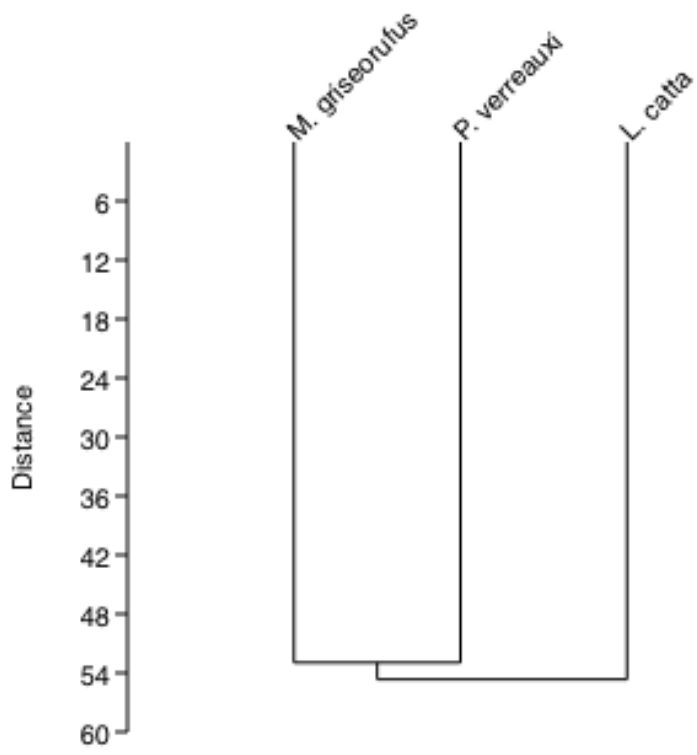
Figure 9. Dendrogram for Beza Mahafaly.

Lemur	Site	Citation
Avahi laniger	Ranomafana	(Faulkner and Lehman 2006)
Cheirogaleus major	Ranomafana	(Wright and Martin 1995)
C. medius	Kirindy	(Fietz and Ganzhorn 1999)
Eulemur rufus	Ranomafana	(Overdorff 1993)
E. rufus	Berenty	(Simmen et al. 2003)
E. rufus	Kirindy	(de Winter et al. 2013)
E. rubriventer	Ranomafana	(Overdorff 1993)
Hapalemur aureus	Ranomafana	(Tan 2000)
H. griseus	Ranomafana	(Tan 2000)
Lemur catta	Berenty	(Simmen et al. 2003)
L. catta	Beza Mahafaly	(Yamashita et al. 2015)
Lepilemur leucopus	Berenty	(Droscher and Kappeler 2014)
Microcebus berthae	Kirindy	(Dammhahn and Kappeler 2008)
M. griseorufus	Beza Mahafaly	(Crowley et al. 2014)
M. murinus	Kirindy	(Dammhahn and Kappeler 2008)
M. rufus	Ranomafana	(Atsalis 1998)
Prolemur simus	Ranomafana	(Tan 2000)
Proplithecus edwardsi	Ranomafana	(Arrigo-Nelson 2006)
P. verreauxi	Berenty	(Simmen et al. 2003)
P. verreauxi	Kirindy	(de Winter et al. 2013)
P. verreauxi	Beza Mahafaly	(Yamashita 2002)
Varecia variegata	Ranomafana	(Balko and Underwood 2005)

Table 1. Citations used for each lemur included in this study.

Species name	Activity pattern	Data available	Citation
Avahi laniger	Nocturnal	Percentage	(Faulkner and Lehman 2006)
Cheirogaleus major	Nocturnal	Presence/absence	(Wright and Martin 1995)
Daubentonia madagascariensis	Nocturnal	None	
Eulemur rufus	Diurnal	Percentage	(Overdorff 1993)
Eulemur rubriventer	Diurnal	Percentage	(Overdorff 1993)
Hapalemur aureus	Diurnal	Percentage	(Tan 2000)
Hpaplemur griseus	Diurnal	Percentage	(Tan 2000)
Lepilemur microdon	Nocturnal	None	
Microcebus rufus	Nocturnal	Percentage	(Atsalis 1998)
Prolemur simus	Diurnal	Percentage	(Tan 2000)
Propithecus edwardsi	Diurnal	Percentage	(Arrigo-Nelson 2006)
Varecia variegata	Diurnal	Percentage	(Balko and Underwood 2005)

Table 2. Activity pattern and data availability for each lemur species in Ranomafana National Park.

Species name	Activity pattern	Data available	Citation
Eulemur rufus	Diurnal	Percentage	(Simmen et al. 2003)
Lemur catta	Diurnal	Percentage	(Simmen et al. 2003)
Lepilemur leucopus	Nocturnal	Percentage	(Droscher and Kappeler 2014)
Microcebus murinus	Nocturnal	None	
Microcebus griseorufus	Nocturnal	None	
Propithecus verreauxi	Diurnal	Percentage	(Simmen et al. 2003)

Table 3. Activity pattern and data availability for each lemur species in Berenty Private Reserve.

Species name	Activity pattern	Data available	Citation
Cheirogaleus medius	Nocturnal	Presence/absence	(Fietz and Ganzhorn 1999)
Eulemur rufus	Diurnal	Presence/absence	(de Winter et al. 2013)
Lepilemur ruficaudatus	Nocturnal	None	
Microcebus berthae	Nocturnal	Presence/absence	(Dammhahn and Kappeler 2008)
Microcebus murinus	Nocturnal	Presence/absence	(Dammhahn and Kappeler 2008)
Mirza coquereli	Nocturnal	None	
Phaner pallescens	Nocturnal	None	
Propithecus verreauxi	Diurnal	Presence/absence	(de Winter et al. 2013)

Table 4. Activity pattern and data availability for each lemur species in Kirindy Forest.

Species name	Activity pattern	Data available	Citation
Eulemur rufus	Diurnal	None	
Lemur catta	Diurnal	Percentage	(Yamashita et al. 2015)
Lepilemur leucopus	Nocturnal	None	
Microcebus griseorufus	Nocturnal	Percentage	(Crowley et al. 2014)
Microcebus rufus	Nocturnal	None	
Propithecus verreauxi	Diurnal	Percentage	(Yamashita 2002)

Table 5. Activity pattern and data availability for each lemur species in Beza Mahafaly Special Reserve.

	A.laniger	E. rufus	E. rubriventer	H. aureus	H. griseus	M. rufus	P. edwardsi	V. variegata
Avahi laniger		38.64	38.64	38.64	38.64	37.44	17.43	38.64
Eulemur rufus	0.301		8.24	21.28	21.28	38.64	38.64	26.19
Eulemur rubriventer	0.163	0.684		21.28	21.28	38.64	38.64	26.19
Hapalemur aureus	0.037	0.088	0.059		3.7	38.64	38.64	26.19
Hapalemur griseus	0.020	0.096	0.067	0.854		38.64	38.64	26.19
Microcebus rufus	0.054	0.084	0.097	0.049	0.080		37.44	38.64
Propithecus edwardsi	0.127	0.136	0.178	0.037	0.020	0.160		38.64
Varecia variegata	0.203	0.316	0.363	0.073	0.078	0.086	0.176	

Table 6. Pairwise comparisons of lemurs in Ranomafana. Divergence distance is shown above the spaces with PS values listed below the spaces.

	C. medius	E. rufus	M. murinus	P. verreauxi
Cheirogaleus medius		38.64	24.99	37.44
Eulemur rufus	0.313		38.64	38.64
Microcebus murinus	0.531	0.656		37.44
Propithecus verreauxi	0.219	0.719	0.625	

Table 7. Pairwise comparisons of lemurs in Kirindy. Divergence distance is shown above the spaces with PS values listed below the spaces.

	E. rufus	L. catta	L. leucopus	P. verreauxi
Eulemur rufus		21.28	38.64	37.44
Lemur catta	0.632		38.64	38.64
Lepilemur leucopus	0.994	0.950		37.44
Propithecus verreauxi	0.133	0.227	0.965	

Table 8. Pairwise comparisons of lemurs in Berenty. Divergence distance is shown above the spaces with PS values listed below the spaces.

	L. catta	M. griseorufus	P. verreauxi
Lemur catta		38.64	38.64
Microcebus griseorufus	0.022		37.44
Propithecus verreauxi	0.125	0.246	

Table 9. Pairwise comparisons of lemurs in Beza Mahafaly. Divergence distance is shown above the spaces with PS values listed below the spaces.

	r	*p*	*n*
Ranomafana	0.5977	0.0013	28
Kirindy	-0.2693	0.8650	6
Berenty	0.9582	0.3278	3
Beza Mahafaly	0.6292	0.3342	6

Table 10. *R* values, *p* values, and number of dyads within each site.

REFERENCES:

Arrigo-Nelson, S. J. (2006). The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' Sifaka (Propithecus edwardsi) in Ranomafana National Park, Madagascar (Dissertation). Stony Brook University.

Atsalis, S. (1998). Feeding ecology and aspects of life history in Microcebus rufus (family Cheirogaleidae, order Primates) (Dissertation). The City University of New York.

Balko, E. A., & Underwood, H. B. (2005). Effects of forest structure and composition on food availability for Varecia variegata at Ranomafana National Park, Madagascar. American Journal of Primatology, 66, 45–70.

Beaudrot, L. H., & Marshall, A. J. (2011). Primate communities are structured more by dispersal limitation than by niches. Journal of Animal Ecology, 80, 332–341.

Cardillo, M., Gittleman, J. L., & Purvis, A. (2008). Global patterns in the phylogenetic structure of island mammal assemblages. Proceedings of the Royal Society B, 275, 1549–1556.

Cowlishaw, G., & Dunbar, R. (2000). Extinction processes. In Primate Conservation Biology. Chicago: The University of Chicago Press.

Crowley, B. E., Rasoazanabary, E., & Godfrey, L. R. (2014). Stable isotopes complement focal individual observations and confirm dietary variability in reddish-gray mouse lemurs (Microcebus griseorufus) from southwestern Madagascar. American Journal of Physical Anthropology, 155, 77–90.

Dammhahn, M., & Kappeler, P. M. (2008). Comparative feeding ecology of sympatric Microcebus berthae and M. murinus. International Journal of Primatology, 29, 1567–1589.

Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences, 104, 13723–13727.

de Winter, I. I., Gollner, A., & Akom, E. (2013). Diet overlap of Propithecus verreauxi and Eulemur rufifrons during the late dry season in Kirindy Forest. Lemur News, 17, 18–21.

Droscher, I., & Kappeler, P. M. (2014). Competition for food in a solitarily foraging folivorous primate (Lepilemur leucopus)? American Journal of Primatology, 76, 842–854.

Elton, C. (1946). Competition and the structure of ecological communities. Journal of Animal Ecology, 15(1), 54–68.

Faulkner, A., & Lehman, S. (2006). Feeding patterns in a small-bodied nocturnal folivore (Avahi laniger) and the influence of leaf chemistry: A preliminary study. Folia Primatologica, 77, 218–227.

Fietz, J., & Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate Cheirogaleus medius: how does it get so fat? Oecologia, 121, 157–164.

Fox, B. J. (1987). Species assembly and the evolution of community structure. Evolutionary Ecology, 1, 201–213.

Gemmill, A., & Gould, L. (2008). Microhabitat variation and its effects on dietary composition and intragroup feeding interactions between adult female Lemur catta during the dry season at Beza Mahafaly Sepcial Reserve, southwestern Madagascar. International Journal of Primatology, 29, 1511–1533.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., Sutherland, M. R., & Irwin, M. T. (2004). Ontogenetic correlates of diet in Malagasy lemurs. American Journal of Physical Anthropology, 123, 250–276.

Houle, A. (1997). The role of phylogeny and behavioral competition in the evolution of coexistence among primates. Canadian Journal of Zoology, 75, 827–846.

Kamilar, J. M., & Beaudrot, L. (2013). Understanding primate communities: Recent developments and future directions. Evolutionary Anthropology, 22, 174–185.

Kamilar, J. M., & Ledogar, J. A. (2011). Species co-occurrence patterns and dietary resource competition in primates. American Journal of Physical Anthropology, 144, 131–139.

Overdorff, D. J. (1993). Similarities, differences, and seasonal patterns in the diets of Eulemur rubriventer and Eulemur fulvus rufus in the Ranomafana National Park, Madagascar. International Journal of Primatology, 14(5), 721–753.

Porter, L. M., Gilbert, C. C., & Fleagle, J. G. (2014). Diet and phylogeny in primate communities. International Journal of Primatology. doi:10.1007/s10764-041-9794-0

Pyron, R. A., Costa, G. C., Patten, M. A., & Burbrink, F. T. (2015). Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. Biological Reviews, 90, 1248–1262.

Simmen, B., Hladik, A., & Ramasiarisoa, P. (2003). Food intake and dietary overlap in native Lemur catta and Propithecus verreauxi and introduced Eulemur fulvus and Berenty, southern Madagascar. International Journal of Primatology, 24(5), 949–968.

Tan, C. L. (2000). Behavior and ecology of three sympatric bamboo lemur species (genus Hapalemur) in Ranomafana National Park, Madagascar (Dissertation). Stony Brook University.

Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. Yearbook of Physical Anthropology, 42, 31–72.

Wright, P. C., & Martin, L. B. (1995). Predation, pollination and torpor in two nocturnal
prosimians: Cheirogaleus major and Microcebus rufus in the rain forest of Madagascar.
Creatures of the Dark: The Norcturnal Prosimians, 45–60.

Wright, P. C., Tecot, S. R., Erhart, E. M., Baden, A. L., King, S. J., & Grassi, C. (2011).
Frugivory in four sympatric lemurs: Implications for the future of Madagascar's forests.
American Journal of Primatology, 73, 585–602.

Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly
Special Reserve, Madagascar. International Journal of Primatology, 23(5), 1025–1051.

Yamashita, N., Sauther, M. L., Cuozzo, F. P., & Jacky, I. A. Y. (2015). Beyond the gallery
forest: Contrasting habitat and diet in Lemur catta troops at Beza Mahafaly Special
Reserve. Folia Primatologica, 86, 35–43.