Phylogenetic systematics and biogeography of lemurs from Madagascar

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Abstract of the Dissertation

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The evolutionary mechanisms influencing biodiversity include abiotic and biotic factors, such as climate change, vicariance, ecological adaptation, and competition. I investigated evolutionary mechanisms that may have influenced the diversity of lemurs from Madagascar by testing geographic and ecological hypotheses in a phylogenetic framework. I used total-evidence methods to infer the lemur phylogeny and divergence times of extant and extinct species. I then tested macroevolutionary hypotheses about lemur biogeography based on the phylogeny to shed new light on the causes of lemur diversification. I examined macroevolution and biogeography at four geographic scales: island-wide, regions, localities, and multiple transects within localities.

I inferred the evolutionary relationships and divergence times of nearly all extant and extinct lemurs (88% of species), as well as a broad sample of their living and extinct relatives. I used a total evidence approach, combining morphological and genetic data, to integrate the phylogenetic and temporal information captured with fossils (369 morphological characters, 5767 molecular characters from multiple independent loci). I found strong support for the phylogenetic relationships among lemurs, even for extinct species. Divergence time estimates for deep nodes were more recent and consistent with the fossil record than published molecular analyses of extant taxa, while divergences closer to the present were in line with previous studies. The divergence time estimate for the Haplorhine-Strepsirrhine split was ~ 60 million years ago (Ma), lemur origins were estimated ~40-50 Ma, and most of the family-level clades diverged after the Eocene-Oligocene boundary. These results have important implications for the diversification dynamics that led to disparities in diversity across the primate tree.

The ecological theory of adaptive radiation predicts identifiable signatures in lineage and phenotypic diversification. I tested the hypothesis that lemurs diversified via an adaptive radiation by quantifying the speciation, extinction, and phenotypic evolutionary dynamics of lemurs and their closest living relatives, the lorisiform primates from Africa and Asia. I found that lemur speciation rates were low at their initial divergence and increased rapidly, with rates of increase slowing towards the present. Remarkably, speciation rates did not decrease towards the present, as would be expected if species richness were ecologically limited. In contrast, the speciation rates of lorisiforms were constant over time, but similar to lemur rates and no significant shift in rates was detected between lemurs and lorisiforms. Body mass evolution followed the predicted “early-burst” pattern of rapid trait divergence followed by a slow-down in trait evolution in lemurs, and phenotypic evolutionary rates differed significantly from the low and constant rates in lorisiforms. Lemurs exhibited the predicted adaptive ecological and phenotypic divergence associated with filling unique adaptive zones. The increase in lemur speciation rates towards the present suggests some processes influenced a continued rise in diversification, such as the late arrival of predators and non-lemur competitors, as well as biogeographic range shifts.

Debate surrounds the relative importance of ecological adaptation compared to vicariant speciation to explain the extraordinary diversity and microendemism in Madagascar. I compared the roles of climate, habitat, geographic dispersal barriers, and interspecies competition in shaping lemur biogeography. I quantified the historical biogeographic patterns of dispersal and vicariance events to infer ancestral ranges and dispersal routes. I measured the taxonomic, phylogenetic, and functional composition of lemur communities from the local to island-wide scales. I found that some rivers were barriers to dispersal between northern and southern regions; however, temporal changes in dispersal probabilities in the Pleistocene did not explain this pattern. The geographic evolution of lemurs included frequent dispersal, especially to and from the central highlands, and high within-region diversification. Founder events and vicariance were less frequent. Biogeographic range shifts during the Oligocene and Miocene were apparent for many clades. The best predictor of phylogenetic community diversity at all scales was primary plant productivity, suggesting that communities with different habitat productivities have been separated longer than predicted by geographic barriers alone. Within local communities, co-occurring species were more distantly related than expected for a randomly assembled community and had high functional trait diversity, suggesting that niche partitioning shapes community composition. The results highlight the importance of including extinct subfossil lemur communities in biogeographic inferences because these phylogenetically and functionally diverse communities were found in the central highlands, where most lemur communities have gone extinct.

While broad-scale differences in habitat and geographic barriers explain lemur community composition across the entire island, interspecific competition is predicted to influence local community assembly the most. I tested the hypothesis that competition is the

dominant process shaping local community assembly. I compared the relative abundances of 13 lemur species on 31 transects along gradients of elevation and resource availability within southeast Madagascar. The functional diversity of communities was quantified based on trait dissimilarity to test for evidence of competition and environmental adaptation. The strongest predictor of lemur diversity was resource abundance. Where resources were most abundant, lemur communities were composed of closely related species that were ecologically dominant. Where resources were scarce, such as at high elevations, communities were composed of distantly related species. Functional diversity was highest where communities were clustered, suggesting character displacement, and lowest where communities were overdispersed, suggesting a few adaptive traits are shared by species. Resource abundance was an important factor shaping local community composition and influencing functional trait patterns.

In summary, for the first time my dissertation research has approached lemur evolution and biogeography from phylogenetic and ecological perspectives to gain an overall picture of the mechanisms driving diversity. I found that the early ecological and phenotypic diversification of lemurs was coupled with increasing speciation rates. Speciation may have been driven by ecological adaptation and geographic range shifts, shaping lemur diversity in deep time. Local community assembly is related to resource abundance and the ability of some species to attain ecological dominance. The results suggest that environment, geography, and interspecies competition have operated at different scales to affect the evolution of lemur diversity.

Dedicated to my hard-working field assistants in Madagascar

Misaotra betsika indrindra

Memorial stone for Dauphin, my field assistant, overlooking his village Tsaramiera and the Faravory river. The morning mist hangs off the cliffs of Tsanganday in the background. Northern Ranomafana National Park, May 17 2013.

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CHAPTER ONE
Introduction

The evolution of biodiversity

Biodiversity is the "currency of life" (Purvis and Hector 2000), and understanding the mechanisms that generate diversity are fundamental to evolutionary and ecological sciences. The evolutionary mechanisms generating biodiversity include abiotic events, such as the emergence of dispersal barriers that split populations and cause allopatric speciation (vicariance). Biotic factors influencing speciation and extinction include ecological adaptation, predator-prey dynamics, interspecies coevolution and competition. As species richness increases, competition for limited resources may result in equilibrium dynamics in speciation and extinction rates over geological time periods and across broad geographic scales (Rabosky and Hurlbert 2015).The ecological limits hypothesis assumes there is a carrying capacity for species diversity related to resource limitation. As diversity approaches equilibrium, speciation and immigration rates are predicted to decrease and/or extinction rates increase, a phenomenon known as diversity-dependence (Rabosky 2009). This concept builds on island biogeography theory (MacArthur and Wilson 1967) and the neutral theories of community assembly (Hubble 2001) to predict that continental species richness is ecologically limited.

In contrast, there may be no equilibrium in species richness because many factors operate to change ecological opportunities at broad temporal and spatial scales (e.g., mass extinctions, key innovations) and there is little evidence that diversity returns to previous levels following perturbation (Harmon and Harrison 2015; Ricklefs and Bermingham 2001). Evidence refuting equilibrium dynamics includes the observation that decreasing taxonomic diversification rates can also be driven by abiotic events such as repeated allopatric speciation (Moen and Morlon 2014), and teasing apart these alternative hypotheses is necessary to understand the causes of changes in diversification dynamics through time. Ecological limits should really apply to local communities in which closely related species actually compete for resources, yet these local communities are rarely at equilibrium (Harmon and Harrison 2015).

Madagascar: a model system

In this dissertation, I investigated multiple evolutionary mechanisms that may have influenced the diversity of lemurs on Madagascar. Lemurs are the only primates on Madagascar, and they are only found there. Lemurs are a monophyletic group, indicating a single origin followed by isolated evolution (Yoder 1994). From this single origin, more than 100 species evolved, and within the last 2000 years, at least 17 giant species have gone extinct (Godfrey et al. 2010; Mittermeier et al. 2010; Schwitzer et al. 2013; Simons et al. 1990). Lemurs belong to the primate clade Strepsirrhini with their sister clade, Lorisiformes, which are broadly distributed through Africa and Asia. Compared to lemurs, lorisiforms have fewer species and are less ecologically diverse (all small, <2kg, nocturnal species feeding on insects, fruits, flowers, and gums). There are no monkeys, apes, or tarsiers on Madagascar, and lemurs fill many niches occupied by other primate groups on continents (Fleagle and Reed 1996). Lemur species richness parallels the diversity seen in continental primate radiations (Table 1.1). Before the extinction of giant species, lemurs spanned the range of body mass seen in all extant primates; from the smallest living primate (~30g mouse lemurs) to the largest living primates (gorilla-sized *Archaeoindris*, ~160kg).

There is no record of lemur evolution between their arrival on the island ~ 50 million years ago (Ma) and the mass extinction of giant forms 2000 years ago, making the evolutionary mechanisms of diversification a mystery. The mass extinction of giant lemurs has reduced diversity dramatically (Godfrey et al. 1999; Wright and Jernvall 1999) and the extant lemurs are the most endangered group of mammals in the world (Schwitzer et al. 2014). To understand the macroevolutionary processes that shaped lemur evolution, I tested geographic and ecological hypotheses related to diversification dynamics, ecological adaptation and niche-filling. I examined macroevolution and biogeography at the island-wide, regional, and local scales to identify how historical processes, ecological divergence and interspecific competition shaped diversity. The results have implications for macroecological and evolutionary hypotheses of species diversification.

Phylogenetics in macroevolution

To test macro-level ecological and evolutionary hypotheses, the species phylogeny, geographic distributions, and functional traits can help distinguish alternate mechanisms potentially driving speciation (Felsenstein 1985; Nunn 2011; O'Meara 2012). Divergence times and branching patterns on phylogenetic trees are indicative of speciation rates (Pybus and Harvey 2000), the timing of divergences in relation to geological phenomena (Yoder and Nowak 2006), and the amount of time for traits to evolve (Revell 2014), species to co-exist (Rabosky et al. 2012) and co-evolutionary forces to operate (Futuyma and Agrawal 2009). Therefore, a robust estimate of the phylogeny and divergence times of study species is fundamental to understanding their evolution.

Molecular data have resulted in many competing hypotheses for lemur evolutionary relationships and divergence times (Horvath et al. 2008). The true phylogeny has been difficult to infer, however, most likely because of the presumed rapid divergence of lineages early in their radiation (Horvath et al. 2008). Further, divergence times have not been calibrated within lemurs because there is no deep-time fossil record of lemur evolution on Madagascar. Lastly, great progress has been made to place the extinct giant lemurs in the tree with both morphological and molecular data (Jungers et al. 1991; Karanth et al. 2005; Kistler et al. 2014). To test hypotheses of evolutionary mechanisms driving the diversification of lemurs, I first inferred a near-complete phylogeny (88% of lemurs), with divergence times based on dozens of calibrations from primate fossils and subfossil lemurs in the tree. I used a total-evidence approach (Ronquist et al. 2012), combining morphological and genetic data, to integrate the phylogenetic and temporal information captured with fossils (370 dental, cranial, postcranial and soft tissue characters, and six molecular loci, for a total of 4,500 characters). I screened morphological data for character independence and partitioned molecular data for fast- and slow-evolving loci. I analyzed the super-matrix with two new dating techniques that calibrate the divergence times with fossils in the tree by inferring morphological substitution rates (Ronquist et al. 2012) and by estimating the speciation and extinction rate of the tree based on fossils (Heath et al. 2014). These methods maximize the information that can be gleaned from fossils.

Adaptive radiation

Madagascar has been isolated from all other landmasses for 80-90 Ma (Samonds et al. 2013), and given that there is no post-Cretaceous fossil record, inferences about the mode of plant and animal origins are largely based on molecular divergence times. Those clades that diverged from mainland ancestors after the break-up of the Gondwanan landmass are inferred to have arrived via dispersal. Only five extant mammalian clades are native, and all postdate the Cretaceous, suggesting their ancestors colonized the insular environment by dispersal, presumably with little competition (Yoder and Nowak 2006). Four of the mammalian clades are monophyletic, supporting the hypothesis that sweepstakes dispersal explains their origins, while only bats probably made multiple dispersals (Yoder and Nowak 2006, Samonds et al. 2013). The primates, called lemurs, most likely arrived shortly after the origins of true primates 50 – 60 Ma, with no mammalian or avian competitors or predators until relatively recently, 5 – 30 Ma, except for the elephant bird which may have been on Madagascar since the Cretaceous (Yoder and Nowak 2006). Lemurs diversified to fill myriad broad- and fine-scale niches in climates ranging from tropical rainforests to deserts. The species richness and natural history of lemurs led to several hypotheses for the mechanisms generating such amazing diversity. A predominant hypothesis explaining lemur diversity posits they evolved via an adaptive radiation (Martin 1972). Lemurs had an ecological opportunity to diversify rapidly when they colonized Madagascar that was unavailable to their mainland relatives. The ecological limits hypothesis predicts that when a clade invades a new adaptive zone, the species carrying capacity changes and new equilibrium dynamics begin (Rabosky and Hurlbert 2015). These equilibrium dynamics supposedly underlie the ecological theory of adaptive radiation (Gavrilets and Losos 2009; Schluter 2000), which predicts that lemurs had increasing speciation and phenotypic evolutionary rates after they colonized Madagascar. Further, lemurs should have had higher taxonomic and phenotypic diversification rates than their mainland sister clade, the lorisiforms, which did not have the same ecological opportunity. As niches filled and a new carrying capacity was reached, these rates are predicted to decline. Alternatively, given the long geological time period of lemur evolution and the large size of the island with its myriad biomes, a signal of early adaptive radiation followed by slow-downs due to equilibrium dynamics may be eroded by ecological factors that continually change the resource base of species (Rabosky and Hurlbert 2015). I tested these hypotheses by estimating the rates of lineage and phenotypic diversification from the phylogeny of strepsirrhines. This comparison of lemur and lorisiform diversification dynamics offers a unique test of the ecological theory of adaptive radiation and ecological limits hypothesis.

Linking historical and ecological biogeography

Changes in diversification rates over time may be driven by biogeographic range evolution. For example, multiple repeated vicariance events can result in an apparent decrease in speciation rates as the splitting of ranges will affect fewer and fewer species (Moen and Morlon 2014). In contrast, dispersal can lead to increases in diversification rates (Fritz et al. 2012). Dispersing into new biogeographic zones may lead to a release from ecological limits in the ancestral range and changes in diversification dynamics (MacArthur and Wilson 1967; Rabosky and Hurlbert 2015), and the susceptibility of communities to invasion by colonists challenges the existence of ecological limits (Harmon and Harrison 2015). Lemurs are an exemplary study system for testing these hypotheses because they are distributed in rainforest, dry deciduous forests, and spiny deserts. The phylogeography of several clades led to the hypothesis that species evolved via ecological speciation into different habitat niches followed by vicariance due to riverine dispersal barriers (Pastorini et al. 2003). Alternatively, microendemism may have resulted from recent vicariance events related to Pleistocene climate oscillations (Wilmé et al. 2006). These alternate hypotheses can be tested using models that explicitly parameterize the likelihood of biogeographic modes of range evolution (e.g., dispersal *versus* vicariance) and the dispersal probabilities among areas (Matzke 2014). Specifically, widespread ancestors should leave descendants with subsets of the ancestral range if vicariance caused cladogenesis, while descendants with ranges outside of the ancestral range indicate dispersal events. I tested alternate biogeographic models of range evolution to clarify the roles of vicariance, dispersal, and ecological limits in generating the diversity of lemurs.

Equilibrium dynamics are also predicted to influence the diversity of regional communities (Rabosky and Hurlbert 2015). For example, the positive relationship between species richness, geographic area and habitat productivity suggest that there is a carrying capacity set by ecological limits of resource availability; larger and more productive areas can support more species before becoming saturated (Hawkins et al. 2003; MacArthur and Wilson 1967). At an ecological time scale, processes limiting species richness may explain this pattern, but consideration of evolutionary time scales suggests that there may be more species in higher productivity areas because of higher diversification rates or longer time in those areas for speciation (Wiens et al. 2010). In Madagascar, ecological limits should result in predictable patterns of community diversity in relation to environmental gradients. If community diversity is limited by resource availability and competition, the taxonomic, phylogenetic and functional diversity of whole communities is expected to be positively related to area and productivity (Graham and Fine 2008). In contrast, there is no expected relationship between phylogeny, functional traits and environment if abiotic factors split populations, and species diverged because they maintained ancestral niches (phylogenetic niche conservatism, Wiens and Graham 2005). I tested the effects of habitat productivity, geographic dispersal barriers, and interspecies competition in shaping lemur biogeography by quantifying the taxonomic, phylogenetic, and functional diversity of 50 modern and five subfossil lemur communities from island-wide to local scales.

Local community assembly

Broad-scale differences in environmental regimes and geographic distance explain lemur community composition across the entire island. Local community assembly within a single regional species pool, on the other hand, is predicted to be affected most by interspecific competition (Cavender-Bares et al. 2004; Kraft and Ackerly 2010; Swenson et al. 2006). Local ecological communities are the level at which ecological limits should apply because this is where species actually interact and compete for limited resources (Cavender-Bares et al. 2009). Earlier studies of niche partitioning among sympatric lemurs suggested that competition was avoided by parsing the environment along temporal, spatial, and dietary axes (Ganzhorn 1997; Ganzhorn 1988; Ganzhorn et al. 1997). I tested the hypothesis that competition is the predominant process shaping local community assembly. I compared the relative abundances of species among transects distributed along gradients of elevation, human disturbance, and resource availability. I quantified lemur abundance as well as the abundance of their preferred food trees on 31 transects within a single region, southeast Madagascar. At this local scale, geographic dispersal barriers should be limited and heterogeneity in resource abundance should be the predominant limitation to lemur diversity (Swenson et al. 2006; Vamosi et al. 2009). I tested the predictions that environmental filtering results in lower phylogenetic community diversity because limiting resources restrict the species that can occur in an area to those sharing adaptive traits shared from common ancestry. In contrast, I tested the prediction that limiting similarity due to competition leads to communities with high phylogenetic diversity because close relatives with similar niches compete and exclude each other, resulting in the co-occurrence of distant relatives.

Summary

My dissertation has approached lemur evolution and biogeography from phylogenetic and ecological perspectives to understand the mechanisms driving diversity at multiple levels. The results clarify the roles of environmental and geographic variables that affected the evolution of lemur diversity at different scales. More broadly, my results suggest that lemur evolution has not been determined by ecological limits; instead, a dynamic history consisting of geographic range shifts, ecological adaptation, and a recent mass-extinction have led to a continuously changing adaptive landscape and increasing speciation rates through time. The implications for global diversity patterns is that multiple processes operate across a continuum of geographic and temporal scales, and understanding the processes requires abandoning a one-size-fits-all-scales model of evolution.

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Tables

Table 1.1.

Comparison of primate diversity globally, illustrating the unique diversity found in Madagascar. Crown group age is based on Springer et al. (2012) except for Lorisiformes and Lemuriformes, for which dates are from this dissertation. Taxonomic richness from the IUCN Red List database (iucnredlist.org, accessed 4/29/2015), updated with the latest taxonomic sources (Mittermeier et al. 2010; Rylands et al. 2012) and to include extinct subfossil lemurs (Godfrey et al. 2010).

Clade	**# Families**	**# Genera**	**# Species**	**Crown age (Ma)**	**Areas occupied**	**Approx. area (10^6 km^2)**
Platyrrhini	4	19	142	23	Central and South America	15
Catarrhini	3	29	146	25	Equatorial Africa, tropical and temperate Asia	7
Tarsiiformes	1	3	10	61	Southeast Asian islands	4.5
Lorisiformes	2	9	28	35	Equatorial Africa, tropical and temperate Asia	7
Lemuriformes	8	21	117	50	Madagascar	0.58

CHAPTER TWO

Combined analysis of living and fossil species to infer the phylogeny and divergence times of lemurs and long extinct primates

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Abstract

Paleontological and neontological systematics seek to answer evolutionary questions with different datasets. Phylogenies and divergence times estimated from exclusively extant or inclusive extant and extinct taxa frequently conflict. Until recently, it was not possible to combine the data from paleontology and neontology to simultaneously estimate evolutionary relationships and divergence times. We used two methods to estimate the phylogeny and divergence times for living and fossil primates, the tip-dating (TD) and fossilized birth-death process (FBD). We collected new morphological data, especially focusing on the living and extinct endemic primates of Madagascar, the lemurs. We combined the morphological data with published DNA sequences to infer near-complete (88% of lemurs) time-calibrated phylogenies. The results suggest that primates originated around the Cretaceous-Tertiary boundary, slightly earlier than indicated by the fossil record and later than previously inferred from molecular data alone. We infer both novel relationships among extinct lemurs, and strong support for relationships that were previously unresolved. Dates inferred with TD were significantly earlier than those inferred with FBD and estimates with FBD were consistent under different fossil date priors. This is the first study to combine morphological and DNA sequence data from extinct and extant primates to infer evolutionary relationships and divergence times, and our results shed light on questions of primate evolution that could not be addressed before.

Keywords: total evidence, primatology, Bayesian phylogenetics, calibration

Introduction

A primary goal of phylogenetic systematics is discovering and describing species, as well as placing them in the Tree of Life (Felsenstein 2004). One impediment to this goal is extinction: more than 90% of species that ever lived on earth are extinct (Novacek and Wheeler 1992). Understanding the evolutionary history of species therefore requires that we have knowledge of extinct taxa (e.g., Pyron 2011). Extinct taxa inform us about the mode of character evolution and transitional forms (Lihoreau et al. 2015; Slater et al. 2012), the timing of species origin and disappearance (Foote 2000), and species distributions in deep time (Patzkowsky and Holland 2012). Unfortunately, biased preservation, incomplete specimens, and the lack of molecular data for comparison to extant species impedes the phylogenetic placement of fossils (Sansom 2015; Wiens and Morrill 2011). Despite these limitations, fossils can give key insights into the phylogenetic placements of living and extinct forms (Pattinson et al. 2015; Wiens et al. 2010; Wiens and Tiu 2012). Until recently, the temporal information captured by fossils was only used to calibrate nodes in a molecular phylogeny based on the assumed position of fossil taxa in extant molecular trees (Parham et al. 2011). Now it is possible to fully capitalize on the wealth of information available from fossils to calibrate trees using the morphological as well as molecular substitution rates (Ronquist et al. 2012a) or estimates of diversification dynamics using all fossils available (Heath et al. 2014). These advances have opened new opportunities to incorporate information from extinct species when inferring phylogenies and divergence times.

Combining morphological and molecular datasets, especially including fossils, can strongly improve phylogenetic inference. Total evidence analyses including extinct taxa have resolved phylogenetic problems as intractable as the relationships of reptiles (Wiens et al. 2010), cetaceans (Spaulding et al. 2009), amniotes (Eernisse and Kluge 1993), wasps (Ronquist et al. 2012a), and spiders (Wood et al. 2012). Several divergence time estimation techniques using fossil taxa integrated in the phylogeny have recently become available (Heath et al. 2014; Pyron 2011; Ronquist et al. 2012a). The first methods, known as “tip-dating” (hereafter TD), use total evidence datasets to model the substitution rate of the molecular and morphological data partitions with extant and fossil tips in the phylogeny (Pyron 2011; Ronquist et al. 2012a). Estimating the rate of morphological evolution is difficult with available Markov *k*-state models, however, and may lead to high error in divergence time estimation (Beck and Lee 2014). Further, TD is useful when morphological data are available, but morphological data may be limited despite a wealth of fossils. In these cases, valuable information about the geographic and temporal distribution of the fossils is lost (Heath et al. 2014). To integrate all available fossil information, a divergence estimation technique was developed to calibrate diversification dynamics (speciation and extinction rates) using all available fossils (fossilized birth-death process, hereafter FBD, Heath et al. 2014). The utility of fossil dating methods in systematics is evident from the recent surge in publications using them (Arcila et al. 2015; Slater 2013; Wood et al. 2012) but the efficacy and comparability of methods has been difficult to quantify (Beck and Lee 2014; Grimm et al. 2014). In this study, we compare the divergence time estimates inferred from total evidence datasets using the TD and FBD techniques on extant and extinct primates, specifically focusing on lemurs of Madagascar.

The systematics of fossil and extant primates have been approached from two perspectives: paleontologists with morphological data and extensive sampling of extinct taxa (e.g., Ni et al. 2013; Pattinson et al. 2015; Seiffert et al. 2010), and neontologists with molecular data for nearly all extant species (e.g., Perelman et al. 2011; Pozzi et al. 2014b; Springer et al. 2012). Divergence time estimates from molecular data are typically older (60 - 80 million years ago, Ma, e.g., Perelman et al. 2011) than the appearance of the earliest true primate fossils ~56 Ma (Beard 2008). This discrepancy may be due to convergent slow-downs in molecular rates (Steiper and Seiffert 2012), the fossil record not capturing the timing of emergence (dos Reis et al. 2014a), or limitations of molecular calibration techniques to maximize the information from fossils (Pyron 2011). In this study, we focus on the latter possibility.

Despite the extensive primate fossil record, multiple fossils are often reduced to calibrations of a single node because only the oldest fossil can be assigned as a minimum age for a node (Ronquist et al. 2012a), e.g., 35 fossil taxa used for 14 node calibrations in Springer et al. 2012). For example, one node calibration used in time-trees is based on two key fossils that are thought to represent the earliest Lorisiformes: *Saharagalago,* and *Karanisia* (e.g., Chatterjee et al. 2009; Horvath et al. 2008; Pozzi et al. 2014a, see Figure 2.1 for taxonomy and simplified phylogeny). Dated at ~37 Ma (Seiffert et al. 2003), these two fossils have only informed a single node – a minimum bound for the divergence between Lorisidae and Galagidae (Pozzi et al. 2014a; Pozzi et al. 2014b; Springer et al. 2012). The crown fossil lorisiforms do not represent the ancestral node themselves, however, because they too share an ancestor with lorises and galagos in the past (Seiffert et al. 2003). Another limitation to node dating is topological uncertainty. The position of 37 Ma North African *Karanisia*, for example, is not resolved and it is possibly a stem strepsirrhine, lemuriform or crown lorisid (Seiffert 2012). Given these caveats, calibrating the Lorisiformes node to the dates of the fossils may be biasing divergence time estimates towards more recent or more ancient dates.

Other fossils have not been informative at all because stem taxa cannot be assigned to a node for calibration. For example, *Djebelemur* is an Eocene African fossil that has been suggested to be a stem strepsirrhine and, as such, has not been informative in divergence time estimation despite its important time period and geographic location (Marivaux et al. 2013). Similarly, the earliest Paleocene/Eocene stem primates (e.g., Plesiadapiformes) and early crown primates (e.g., Adapiformes) have had no bearing on the dating of the primate phylogeny because the taxa fall outside the crown group and cannot be assigned to nodes for calibration. The lemurs of Madagascar are especially intractable with respect to fossil calibration because there are no true fossil lemurs. There are, however, 17 species of extinct lemurs that are subfossils dating from 400 – 20,000 years ago (Godfrey et al. 2010). Calibrations of lemur divergence times have used multiple primate and nonprimate outgroups (Horvath et al. 2008; Yoder and Yang 2000) and divergence times for extinct subfossils were estimated from phylogenetic bracketing until recently (Catlett et al. 2010), but newly published ancient DNA has allowed the subfossils to be placed in the tree with great precision (Kistler et al. 2015). To close the gap between neontology and paleontology, we focus on the strepsirrhine primates: Lemuriformes from Madagascar and Lorisiformes from Africa and Asia. We include 33 extinct primates, focusing on the earliest true primates, stem strepsirrhines and subfossil lemurs. This is the first inference of primate phylogeny and divergence times with combined morphological and molecular data including fossils actually in the tree.

Lemurs are a monophyletic radiation of primates that diverged from their closest relatives, the lorisiforms, between 50 and 70 Ma based on node-calibrated molecular divergence time analyses (Fabre et al. 2009; Horvath et al. 2008; Kistler et al. 2015; Perelman et al. 2011; Pozzi et al. 2014a; Yoder and Yang 2000). Living lemurs are species-rich (99 species currently recognized, Schwitzer et al. 2013, IUCN Red List database, www.iucnredlist.org accessed February 28 2015), in addition to the 17 recently extinct species. Molecular analyses conflict regarding the placement of major clades, including the earliest diversification of taxonomic families characterized by short internodes and long branches (Horvath et al. 2008; Perelman et al. 2011; Springer et al. 2012; Yoder and Yang 2000; Yoder 1994). The placement of the extinct giant lemurs in the phylogeny was originally based on the morphometric affinities of the extinct lemurs to living species (e.g., Jungers et al. 1997; Jungers et al. 1991). Fragments of ancient mitochondrial DNA (Karanth et al. 2005; Orlando et al. 2008), and, more recently, the entire mitochondrial genome for five taxa (Kistler et al. 2015) supported or overturned some of these relationships. The molecular and morphological data for living and extinct lemurs have not been combined in phylogenetic analyses to exploit all the available data. Finally, a complete phylogeny is ideal for comparative analyses of trait evolution and diversification because missing species bias the inferences of evolutionary events (Cusimano et al. 2012). In this study, we infer a near-complete phylogeny of extant and extinct lemurs and their closest relatives with a combined morphological and molecular dataset. We date the tree by calibrating substitution rates using a large sample of extinct early primates that are tips in the phylogeny to maximize the information obtained from fossils. This study is the first to jointly evaluate the relationships and divergence times of extinct and extant lemurs, and the results change the mode and tempo of lemur diversification.

Materials & Methods

The methods follow the schematic given in Figure 2.2.

Taxonomic sampling

The taxonomy of lemurs has changed with the increase in DNA sequences to delimit many cryptic species that were previously subsumed as single species. The most recent taxonomic compilation recognizes 97 species of living lemurs (Mittermeier et al. 2010), with two new species described since then (Rasoloarison et al. 2013; Thiele et al. 2013) for a total of 99 lemur species (IUCN Red List). Our dataset included 87 living lemurs (~87.88% of recognized living lemurs), and 14 extinct lemurs (82.35%, Godfrey et al. 2010). We also included a subset of other primates, including the closest extant relatives of lemurs, the Lorisiformes (67.85% of 28 IUCN recognized species), and eight haplorhine primates (< 3% of 294 IUCN recognized species). Fossil taxa included the following: four crown and two potential stem strepsirrhines, five adapiforms, two fossil haplorhines, three early primates of disputed phylogenetic placement, and three stem primates (Figure 2.1, Table 2.1). The complete data matrix included 148 taxa.

Morphology

For 47 taxa (16 extinct, 31 extant), we collected morphological data *de novo* from osteological museum specimens, casts and photographs of original specimens, with multiple specimens examined when possible to reflect variation and polymorphisms. The sample size per species varied with the availability of specimens; for example, some species were represented by a single specimen while others were scored for between five and 10 specimens. We supplemented the new dataset with data from the literature for 20 fossil taxa and 19 extant taxa (Seiffert et al. 2015; Ni et al. 2013). The total morphological dataset included 85 taxa.

The starting point for scoring characters was a morphological matrix with 421 characters from previous studies (Appendix I, Cartmill 1975; Cartmill 1978; Groves and Eaglen 1988; Groves and Helgen 2007; Groves and Trueman 1995; Ni et al. 2013; Rasoloarison et al. 2000; Seiffert et al. 2015; Tattersall and Schwartz 1974; Tattersall and Schwartz 1991; Yoder 1994). Characters included binary and multi-state traits describing cranial and long bone features such as crests, processes, and foveae, the presence, number and orientation of foramina. Dental characters included the presence/absence, relative orientations and development of teeth, cusps, crests, cristae/ids, conules and cingula/ids. We included eight quantitative measurements that were size-adjusted by dividing each variable by the geometric mean of all variables, and then converted to discrete states using gap-coding (Thiele 1993). Polymorphisms were scored as unique states as in Seiffert et al. (2015) to incorporate the polymorphic information in the dataset (Wiens 2000). All characters were treated as unordered. For the taxa scored *de novo*, we were able to collect data on 40 – 50% of the 421 characters, principally cranial and dental characters and postcranial characters characterizing the long bones. Missing data ranged from <1% to 95% (Appendix I Table 1). All the data have been deposited in the online database MorphoBank (www.morphobank.org, project#2167).

To test the assumption of character independence in the morphological dataset, we converted the original matrix into a matrix of binary states for the same (1) or different (0) character states among pairs of species. We then calculated the Gower dissimilarities of characters to determine if there were characters that had dissimilarities of 0 (*daisy* function in the cluster package of the R statistical environment, R Core Team 2014, and code from Dávalos et al. 2014). Dissimilarity scores of 0 indicate that the character pair has identical state changes among species; i.e., there is possible character dependence. For those pairs of characters that had

0 dissimilarity, we omitted one from each pair, choosing the character that showed the most 0 dissimilarities with other characters in the dataset. Fifty-two characters were found to have identical state distributions among species, suggesting dependence, and we excluded those characters (Appendix I). Here, we report the results from the reduced dataset (369 characters), while results analyzing the complete morphological dataset are included in the Appendix I.

Molecular data

We compiled published molecular sequences from GenBank or directly from first authors for six protein-coding loci chosen to maximize overlapping coverage among study species, including two mitochondrial loci (mtDNA: *cytocrhome b* and *NADH dehydrogenase - 4*) and four nuclear loci (nDNA: *adenosine A3 receptor, cannabinoid receptor 1, and recombination activating gene 1* and *2*, 5767 characters, Chatterjee et al. 2009b; Fabre et al. 2009; Horvath et al. 2008; Kistler et al. 2015; Perelman et al. 2011; Pozzi et al. 2014a; Springer et al. 2012; Yoder and Yang 2000). Sequences for each locus were aligned using amino acid translation alignment in MAFFT (Katoh et al. 2005) as implemented in Geneious software v.7.1.7 (Kearse et al. 2012). Alignments were verified and edited manually as necessary (www.morphobank.org, project #2167). We concatenated and partitioned the molecular dataset using likelihood statistics, as implemented in PartitionFinder software (*greedy* search algorithm, Lanfear et al. 2012, Appendix I).

Phylogenetic inference

We jointly inferred the phylogeny and divergence times by conducting Bayesian analyses of the total evidence dataset using MrBayes v3.2.2 (Ronquist et al. 2012a; Ronquist et al. 2012b). We used both the TD and FBD approaches to calibrate the divergence time estimates with the dates of fossil taxa included in the dataset. The TD analysis parameterizes the substitution rate of the morphological data partition as well as the molecular data, maximizing the information content of the fossil and subfossil taxa in ways that have never been possible for strepsirrhines before. The FBD analysis estimates speciation, extinction, and preservation parameters from the fossil data to calibrate the diversification rate of the tree and therefore the divergence times, rather than the substitution rates of morphological characters themselves (Heath et al. 2014). In the original implementation of the FBD method, the taxonomic association of fossils to living clades is specified *a priori*, similar to node - dating. In MrBayes v3.2.2, the phylogenetic position of fossils is inferred from the morphological data partition. The fossil dates were taken from the literature (Table 2.1). We used a uniform prior between the minimum and maximum fossil ages when these dates were available, or a fixed prior when only one date was available. Dates were first taken from the Paleobiology database (Behrensmeyer and Turner accessed 2015) and verified with primary and secondary literature, especially Hartwig (2002) and references therein, and Godfrey et al. (2010). To evaluate the effects of prior date distribution on divergence time estimates, we ran two FBD analyses with the same settings and data as above, one with wide distributions based on coarse-scale references (Behrensmeyer and Turner accessed 2015) and one analysis with only fixed point estimates on divergence dates. To account for the possibility that fossils occurred outside the precise temporal window of their localities, we present the results with prior distributions. We set *Purgatorius* as the outgroup because it is the earliest known possible stem primate or stem euarchontan (Hartwig 2002; Rose 2006).

Clock model comparison

To compare clock models, we used the stepping - stone approach implemented in MrBayes v3.2.2 to calculate the marginal likelihoods of the data under the strict molecular clock model and the following relaxed - clock models: Brownian motion (TK02), inverse gamma rates (IGR), and Compound Poisson Process (CPP, Ronquist et al. 2012a). Stepping - stone analysis uses

Metropolis chain Monte Carlo (MCMC) to estimate the likelihood of the given model close to the posterior distribution and at intervals approaching the prior distribution, making it an accurate measure of marginal likelihoods for Bayes factor model comparison (Xie et al. 2010). Models were compared to each other (likelihood of model 1 / likelihood of model 2), and models with Bayes factor ratios greater than 3 were considered better models (Kass and Raftery 1995). We ran stepping - stone analyses for 50 steps of 2.5 million generations each, sampling every 25000 generations and discarding the first step and first 10% of each subsequent step as burn-in.

Model specifications

The model of evolution for each data partition was specified *a priori* using the results of the optimal model tests for the molecular dataset and the Markov-*k* model of morphological evolution (standard variable model, Lewis 2001). Shapes of the gamma distributions of rate variation among characters, substitution rates and state frequencies were unlinked among data partitions. We ran two independent MCMC searches with four separate chains of 60 - 70 million generations, sampling every 5,000 generations. Three chains were heated (temperature = 0.01) and one was cold which recorded the model parameters. We used the following prior parameter settings: variable rate prior, uniform clock branch length prior, Brownian motion (TK02) relaxed clock model with values chosen from an exponential distribution with a rate parameter of 10, and a gamma-distributed clock rate adjusted according to the number of data partitions such that the shape parameter was 0.666 and the rate parameter was 1.33 (following dos Reis et al. 2014b). This prior placed the highest prior probabilities on substitution rates in the range of 1E-2 to 1E-3 substitutions/site/million years, in line with previous studies of primate molecular evolution (Yang 2008; Yoder and Yang 2000). The FBD analysis included additional parameters with the following prior settings: exponentially-distributed speciation prior (rate = 20), beta-distributed extinction and fossilization priors (shape and rate = 1), 'samplestrat' parameter set to 'fossiltip' to indicate the fossil lineages ending in distinct tips rather than as ancestors, and sample probability of 0.25 (a low probability of fossil sampling, considering the comparatively low number of fossils included in this study compared to all fossil primates). MrBayes3.2.2 was run through the CIPRES Science Gateway (Miller et al. 2010). The concatenated datasets with MrBayes codes for conducting the analyses described above were deposited in the MorphoBank project (www.morphobank.org, project#2167).

We verified convergence of the MCMC search by: 1) plotting the time series of parameter values sampled from each chain; 2) quantifying the effective sample sizes (ESS) for all model parameters, representing the number of independent estimates of the parameter values drawn from the posterior, with ESS values >200 being ideal (quantified in Tracer v1.6, Rambaut et al. 2014); 3) verifying the standard deviation of split frequencies (SDSF) were <0.01 and potential scale reduction factor (PSRF) values were stable around 1.00; and 4) examining the split frequencies among chains and generations using the utilities in the online application Are We There Yet (Nylander et al. 2008). For all parameters, independent runs had sufficient mixing, SDSF < 0.01, PSRF ~1, and reached stationarity by ~30 million generations. We discarded the first 50% of generations as burn-in and summarized the posterior distribution of topologies as the mean clade credibility (MCC) tree.

Our goal was to quantify the divergence times for primates using methods that incorporate fossils in the phylogeny. We compared the fit of the data to the two models (TD and FBD) based on their marginal likelihoods, estimated using the stepping - stone analyses described above. We compared the dates inferred from the two methods for 21 nodes of interest by extracting the median age estimates and the low and high estimates from the 95% highest probability distribution (HPD). We then used a paired-sample t - test to test for a difference in the median age estimates from the two methods.

Results

Relaxed-clock models

The relaxed-clock model with the highest marginal likelihood was the TK02 model, although the Bayes factor ratios of the alternative models to the TK02 model were ~ 1, indicating there was not strong evidence for the TK02 model being a better fit to the data than other models. The strict clock model had the lowest marginal likelihood and may make unrealistic assumptions about the constancy of molecular evolutionary rates across the tree (Drummond et al. 2006), and other models were more complex than the TK02 but did not explain the data better than the simpler model. We therefore chose the TK02 model for further analyses.

Parameter rate estimates

Rate estimates for model parameters were consistent across analyses. The 95% highest probability distribution (HPD) of substitution rate estimates for the molecular partitions were 0.35-0.38 substitutions/site/Ma for the slow - evolving partition (nuclear genes, 1st and 2nd codon positions of *cytochrome B*, 2nd and 3rd codon positions of *NADH dehydrogenase - 4*), and 3.99-4.24 sub./site/Ma for the fast evolving partition (3rd codon position of *cytochrome B,* 1st codon position of *NADH dehydrogenase – 4*). The morphological partition substitution rate was intermediate, at 2.22-2.63 sub./character/Ma. The mean TK02 variance parameter of ~0.2 (95% HPD 0.08-0.38) and the clock rate parameter of ~1.2e-2 (8e-3-1.2e-2) indicated low rates of change across the tree. The net speciation rate estimate from the FBD analysis was 0.06 (0.03-0.11), the relative extinction rate was 0.75 (0.40-0.96), and the relative fossilization rate was 0.09 (0.004-0.33).

Phylogenetic inferences

The data under the FBD model had a higher average marginal likelihood (-86906.6) than under the TD model (-86916.2), although the Bayes factor ratio of ~1 suggests the models do not differ in their fit to the data (following Kass and Raftery 1995). The MCC trees generated from the TD and FBD analyses differed in the topology inferred for some fossil taxa, and those nodes had low posterior probabilities (Table 2.3, Figure 2.3, Appendix I Figures 1-3).

Divergence time inferences

The divergence times estimated from the TD were significantly older than those estimated from FBD (Figure 2.4, mean difference = 8.85 million years older, paired-sample t-test, $t_{20} = -9.21$, $p < 0.001$), and the TD dates were older than previously inferred using node dating (Table 2.4, Appendix I Table 3). The results of the FBD analysis with wide and fixed date priors are comparable, with a mean difference in the median estimates of 0.53 Ma, and the 95% HPD range was 1 Ma wider on average with fixed dates compared to HPDs estimated using age distributions (Appendix I Table 3).

Discussion

The new phylogenies for lemurs we inferred are the most taxonomically complete to date, including representatives of every genus of extant and extinct lemurs as well as inferring the positions of these taxa with strong support. These nearly complete combined analyses of living and extinct lemurs as well as multiple fossils illuminate the relationships among living and extinct forms and their divergence times. We estimated a post-Cretaceous split between Haplorhini and Strepsirrhini, instead of the pre-Cretaceous dates usually inferred from molecular data. Further, for the lemurs that have no fossil record until the Holocene, we inferred divergence times for the clade that are more recent than previously estimated from molecular data only. The divergence of the families was concentrated around the Eocene-Oligocene boundary, a geological time period associated with major faunal turnover in many primate clades (Seiffert 2007). These results have implications for the drivers of diversification in primates, especially extant and extinct lemurs.

Joint inference of phylogeny and divergence dates: ancient primate fossils

Support for the phylogenetic placement of stem and early primate fossil taxa was weak, and this was expected given that many taxa had high proportions of missing data and apomorphic character states (e.g., *Altiatlasius,* some adapiforms). Including them in these analyses allowed us to place the taxa in the tree with empirical data and the temporal occurrence information of the fossils calibrated the speciation and extinction rates of the tree. This is the first study that could use the temporal information of stem primates, particularly the oldest known fossils, in estimates of divergence times. Some inferred relationships were unexpected and most likely due to the paucity of fossils in this sample compared to previous studies focused on fossils (e.g., Seiffert et al. 2012). For example, some fossil clades which are considered to be closely related to crown clades were inferred to be outside crown Haplorhini and Strepsirrhini, most notably the Adapiformes (sister to Strepsirrhini, Seiffert et al. 2009), and the Omomyiformes (*Teilhardina* sister to Haplorhini Beard 2008; Hartwig 2002*, Altiatlasius* sister to Anthropoidea, Ni et al. 2013). The underrepresentation of omomyiform and adapiform species in the present sample precludes conclusions regarding relationships for those taxa. Including these earliest primate taxa however, allowed us to estimate the rate of morphological substitution as well as speciation and extinction rates to calibrate divergence times.

The divergence times we estimate with the FBD model for the deepest nodes are generally more recent than previously suggested using molecular data for only extant taxa. Total evidence dating techniques do not assume that fossil species represent minimum ages for the most recent common ancestors (MRCAs) of living taxa, as node dating does. Rather, the fossil taxa share a common ancestor with sister lineages sometime before their appearance in the record (Ronquist et al. 2012a). Fossil taxa represent a minimum bound for a node, but the maximum bound may be much earlier than allowed by most hard prior distributions used to date. Our results suggest the divergence of Haplorhini and Strepsirrhini around the Cretaceous - Tertiary boundary ~60 - 70 Ma, with a rapid subsequent divergence among lineages during the Paleocene. These dates are more concordant with the fossil record than the deep Cretaceous estimates found by some molecular studies (Horvath et al. 2008; Perelman et al. 2011a; Wilkinson et al. 2010). The origin of strepsirrhines is still poorly understood. In this analysis, the djebelemurid clade of northern Africa is the oldest stem strepsirrhine known at approximately 45-49 Ma (Marivaux et al. 2013; Seiffert 2012). Djebelemurid fossils have not been informative for studies using node dating because they cannot be assigned to any node in extant-only phylogenies. Our inference of strepsirrhine divergence times offers a unique perspective that has been impossible in previous studies.

Joint inference of phylogeny and divergence dates: Strepsirrhini in general and Lemuriformes in particular

Total evidence analyses can test the assumption that the placement of fossil taxa in the phylogeny corresponds to nodes linking extant taxa. An especially important example of fossils representing minimum age bounds in this dataset concerns the MRCA of Lorisiformes, which was previously calibrated to approximately 37 Ma based on *Saharagalago* and *Karanisia* (Pozzi et al. 2014a; Seiffert et al. 2003). In our analyses, in contrast, the relationships of these fossils and their MRCAs with crown sister lineages were inferred from the data, and the results show these fossils shared a common ancestor with crown lorisiforms ~38-50 Ma. Given the differences in node-dating and total evidence methodology, it is encouraging that we inferred the split between lorises and galagos ~35 Ma because concordance of estimates across methods is strong evidence for these inferences.

This study is the first to infer the position of subfossil lemurs and their divergence times jointly from empirical analysis of combined data. The strepsirrhine phylogenies were generally well-supported, especially at key nodes within Lemuriformes that have been contentious until now. Extinct species were placed with moderate to strong support. The phylogenetic relationships we inferred corroborate inferences from both morphological affinities (e.g., Jungers et al. 1997; Jungers et al. 1991) and ancient DNA (Karanth et al. 2005; Orlando et al. 2008) for most lineages (e.g., Archaeolemuridae, Palaeopropithecidae, *Pachylemur, Daubentonia robustus*).

The placement of *Megaladapis* as sister to all lemurs other than *Daubentonia* conflicts with its morphological similarities to *Lepilemur* (e.g. Tattersall and Schwartz 1974), and the sister relationship to Lemuridae found with ancient mitochondrial DNA. This result was surprising, given that we included the published molecular data that had recovered the *Megaladapis*+Lemuridae relationship (Kistler et al. 2015). Differences in data partitioning may explain the discrepancy among studies; previous studies had applied a single molecular model to the entire mitochondrial genome or partitioned the genome by codon position (Kistler et al. 2015), instead of partitions based on the best subset of substitution rate categories as in this study. The specification of molecular models in phylogenetic inference is an important yet often overlooked issue, and misspecification of the molecular partitions and models can lead to poor inferences (Brown and Lemmon 2007, Lanfear et al. 2012). In this study, the best partitioning scheme of the multi - gene alignment included a fast - evolving partition (*cytochrome B* third codon position and *NADH dehydrogenase 4* first codon position), and a slow-evolving partition (all other loci together). These differences in molecular evolution models and partitioning scheme between previous studies and this study may account for the discrepancies in fossil placement observed.

The divergence dates for lemurs using TD were in general much older than those inferred from FBD and previous estimates from node dating. We estimated the divergence of *Daubentonia* from the rest of Lemuriformes to 55-63 Ma using TD, and 45-50 MA from FBD (Table 2.3). Node-calibrated molecular phylogenies dated the subsequent divergence of lemur families to ~30-40 Ma, and the relationships among families were unresolved or conflicting (Chatterjee et al. 2009a; Horvath et al. 2008; Perelman et al. 2011a; Yoder and Yang 2004). Our TD analysis suggests the divergences among families occurred ~40-50 Ma, while the FBD analysis inferred divergence times ~30-40MA, in line with previous node-dating results (Table 2.4). Recent studies using the TD method have also recovered earlier dates than those inferred using node dating (Beck and Lee 2014a; Ronquist et al. 2012a; Slater and Harmon 2013; Slater et al. 2012; Wood et al. 2012). The TD total evidence method may overestimate divergence times because the Markov-*k* model of discrete morphological evolution may underestimate the morphological rate of change (Beck and Lee 2014a). We found that the morphological substitution rate was intermediate between the slowest and fastest evolving molecular partitions. If there is character state saturation in the morphological data, the same character states will appear in different species through homoplasy, leading to underestimated rates of morphological substitution (Wagner 2000), and in turn to overestimated dates. These observations may explain the late dates from TD and why the dates inferred in the FBD analysis were more consistent with node-dating results.

We argue that the benefits conferred by the ability to place important extinct taxa (e.g., *Djebelemur, Wadilemur, Komba,* extinct lemurs) outweigh the disadvantages of the artifacts that drive the differences between TD and FBD, especially in comparison to node-based divergence times from extant-only datasets. Previous molecular analyses could not include calibration information for stem taxa like adapiforms or *Djebelemur*, despite the importance of these fossil taxa in the evolution of primates. Further, the lack of fossils limited node-calibrated molecular analyses of lemurs. The divergence times of extinct and extant lemurs were recently inferred from mitochondrial genomes and the results were similar to those we report, with the exception of the position and divergence time of *Megaladapis* (Kistler et al. 2015) as noted above. Mitochondrial genomes are known to reach coalescence faster than nuclear genomes, leading to saturation and bias in divergence times towards the calibration points; divergences that are older than calibration points are underestimated and younger divergences are overestimated (Arbogast et al. 2002; Zheng et al. 2011). The four node calibrations used previously (Kistler et al. 2015) were based on fairly recent divergences in the Haplorhini (human-chimp ~ 5-8 Ma, baboons ~ 1-3.5 Ma), and two older calibrations (apes-Old World Monkeys ~ 21-34 Ma, Lorisiformes ~ 37 Ma). If divergence times previously derived from mitochondrial DNA sequences were biased towards calibration points, then the inferred divergences of lemurs should be close to those calibrations, which they are (Table 2.4). We included the mitochondrial sequences from previous studies, and combined them with morphological data that are most likely coded by multiple nuclear loci. In addition, with our calibrations based on 33 fossils actually in the tree, spread across the chronology of early to recent primate diversification, it is expected that lineage divergence times should be earlier and spread more evenly through time than observed in the mitochondrial node-dating divergence estimates, which is the case in our results.

This study is the first to infer lemur evolutionary relationships and divergence times from combined paleontological and neontological data. This is also the most complete phylogenetic inference for lemurs to date. Accurate and complete dated phylogenies are necessary for testing hypotheses about lineage and character evolution (Felsenstein 1985; Nunn 2011). Our time-tree inferences have important implications for the diversification dynamics in this biologically diverse and endangered primate group. For example, the tree shape and balance is indicative of the tempo of diversification and possible shifts in diversification rate through time (Pybus and Harvey 2000; Rabosky 2014). Including fossil species in phylogeny-based inferences of lineage diversification rates is at the forefront of macroevolution (Pyron and Burbrink 2012; Silvestro et al. 2014). With increasing availability of molecular and morphological data, paleontological databases, and innovative models of divergence times and character evolution, researchers in phylogenetic systematics and macroevolution are primed to clarify the structure and the ages of the tree of life.

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Tables and figures

Table 2.1.
Fossil taxa included in phylogenetic analysis and age-range used for divergence-time estimation.

Genus	Species	Min age (Ma)	Max age (Ma)	Reference
Adapis	*parisiensis*	33.9	41.3	1,2
Aegyptopithecus	*zeuxis*	28.1	33.9	1,2
Altiatlasius	*koulchii*	56	59.2	1,2
Anchomomys	*frontanyensis*	37.2	48.6	1,2
Archaeoindris	*fontoynonti*		0.002149	3
Archaeolemur	*edwardsi*		0.001	3
Archaeolemur	*majori*		0.0014	3
Babakotia	*radafolia*		0.00484	3
Branisella	*boliviana*	26.4	26.4	2
Cantius	*abditus*	50.3	55.8	1,2
Carpolestes	*simpsoni*	55.8	56.8	2
Daubentonia	*robustus*		0.001	3
Djebelemur	*martinezi*	41.3	56	1,2
Donrussellia	*provincialis*	48.6	55.8	1,2
Hadropithecus	*stenognathus*		0.0016	3
Karanisia	*clarki*	33.9	38	1,4
Komba	*sp.*	20	22.4	1,2
Leptadapis	*magnus*	33.9	41.3	1,2
Megaladapis	*edwardsi*		0.001	3
Megaladapis	*grandidieri*		0.001	3
Megaladapis	*madagascariensis*		0.00276	3
Mesopropithecus	*pithecoides*		0.0014	3
Mesopropithecus	*dolichobrachion*		0.0014	3
Nycticeboides	*simpsoni*	5.3	11.6	2
Pachylemur	*insignis*		0.0117	3
Palaeopropithecus	*ingens*		0.001	3
Palaeopropithecus	*maximus*		0.00216	3
Plesiadapis	*tricuspidens*	56	58.7	1,2
Plesiopithecus	*teras*	28.1	33.9	1,2
Pronycticebus	*gaudryi*	38	47.8	2
Purgatorius	*unio*	63.3	66	1,2
Saharagalago	*misrensis*	33.9	38	1,4
Teilhardina	*americana*	50.3	55.8	1,2
Wadilemur	*elegans*	28.1	33.9	1,4

1: Behrensmeyer and Turner accessed 2015, 2: Hartwig 2002, 3: Godfrey et al. 2010, 4: Seiffert et al. 2003

Table 2.2.
Marginal likelihood of each clock model for divergence-time estimation, calculated as the average of the summed marginal likelihoods across 50 steps of a stepping-stone analysis. Each model is compared to the model with the lowest marginal likelihood (TK02) with Bayes factor ratios (alternate model likelihood / TK02 likelihood). Though the TK02 model had the highest marginal likelihood, exceeding the next-best model (CPP) by ~54 log likelihood units, the Bayes factor ratio ~1 indicates a similar fit of the data to the different clock models.

Model	**Marginal likelihood (ln)**	**Bayes factor ratio (alternate model / TK02)**
TK02	-89920.95	-
CPP	-89974.63	1.00
IGR	-90030.54	1.00
Strict	-90134.51	1.00

Table 2.3.
Summary of the phylogenetic placement of taxa in this study compared to previous hypothesized topologies.

Taxon	**Previous placement**	**Ref**	**TD placement**	**FBD placement**
Stem primates, Plesiadapiforms: *Purgatorius*, *Carpolestes*, *Plesiadapis*	Outside crown primates	1	Outside crown primates	Outside crown primates
Early primates: *Donrussellia*	Adapiformes	2	Sister to Adapiformes	Sister to Adapiformes
Teilhardina	Omomyiformes, Sister to Tarsiidae	3	Sister to Primates	Sister to Primates
Altiatlasius	Problematic, possibly Omomyiformes	2	Sister to Primates	Sister to Primates
Adapiformes	Sister to Strepsirrhini Sister to Haplorhini	2,4	Outside crown Primates	Outside crown Primates
Djebelemur	Sister to Strepsirrhini (Stem Strepsirrhini)	5	Sister to Lorisidae (Crown Strepsirrhini)	Sister to Strepsirrhini
Plesiopithecus	Sister to *Daubentonia* (Lemuriformes), Lorisiformes	4,6	Sister to *Daubentonia*	Sister to Strepsirrhini
Wadilemur	Crown Lorisiformes, stem galagid	7	Sister to Galagidae	Sister to Galagidae
Komba	Crown Lorisiformes, stem galagid	7	Sister to *Euoticus* (crown Galagidae)	Sister to *Euoticus* (crown Galagidae)
Nycticeboides	Sister to *Nycticebus* (crown Lorisidae)	7	Sister to *Nycticebus* (crown Lorisidae)	Sister to *Nycticebus* (crown Lorisidae)
Saharagalago	Crown Galagidae	8	Sister to Lorisiformes	Sister to Lorisiformes
Karanisia	Crown Lorisidae	8	Sister to Lorisiformes	Sister to Lorisiformes
Lorisidae / Galagidae	Paraphyletic, monophyletic	9,10	Monophyletic	Monophyletic

Taxon	**Previous placement**	**Ref**	**TD placement**	**FBD placement**
Daubentonia robustus	Sister to *Daubentonia madagascariensis*	11	Sister to *D. madagascariensis*	Sister to *D. madagascariensis*
Megaladapis	Sister to Lepilemuridae Sister to Lemuridae	12-14	Sister to all lemurs *sans Daubentonia*	Sister to all lemurs *sans Daubentonia*
Archaeolemuridae	Sister to Palaeopropithecidae + Indriidae	11,13,14	Sister to Palaeopropithecidae + Indriidae	Sister to Palaeopropithecidae + Indriidae
Palaeopropithecidae	Sister to Indriidae	11,13-15	Sister to - Indriidae (Indriidae paraphyletic with *Indri* sister to Palaeopropithecidae)	Sister to Indriidae
Pachylemur	Sister to *Varecia,* Lemuridae	11,13	Sister to *Varecia,* Lemuridae	Sister to *Varecia,* Lemuridae
Hapalemur simus	*Hapalemur* paraphyletic, *H. simus* sister to *Lemur catta*	16	*Hapalemur* monophyletic, *H. simus* sister to other *Hapalemur*	*Hapalemur* monophyletic, *H. simus* sister to other *Hapalemur*
Phaner	Cheirogaleidae Lepilemuridae	17-19	Sister to Cheirogaleidae	Sister to Cheirogaleidae

1: Bloch et al. 2007; 2: Hartwig 2002; 3: Beard 2008; 4: Godinot 2005; 5: Marivaux et al. 2013; 6: Simons & Rasmussen 1994; 7: Seiffert et al. 2005; 8: Seiffert et al. 2003; 9: Yoder et al. 2001; 10: Masters et al. 2005; 11: Godfrey et al. 2010; 12: Tattersall & Schwartz 1974; 13: Kistler et al. 2014; 14: Karanth et al. 2005; 15: Jungers et al. 1991; 16: Pastorini 2000; 17: Tattersall & Schwartz 1991; 18: Horvath et al. 2008; 19: Springer et al. 2012

Table 2.4.
Comparison of divergence time estimates at key nodes in the phylogeny. The results of this study using the fossilized birth-death process and combined data are compared to those published previously using node-dating and molecular data. Cells marked with an asterisk were used as node calibrations in previous studies.

Node	**This study**	**Kistler et al. 2015**	**Yoder and Yang 2004**	**Horvath et al. 2008**	**Perelman et al. 2011**	**Springer et al. 2012**	**Chatterjee et al. 2009**
Haplorhini/ Strepsirrhini	61 (55,69)	68 (60,76)	85* (77,90)	-	87 (76, 99)	68 (63,71)	67 (64,73)
Crown Strepsirrhini	54 (48,63)	59 (52,66)	69 (61,75)	75 (67,84)	69 (59,77)	54 (53,55)	52 (48,56)
Lorises + Galagos	35 (31,38)	38* (37,41)	39* (38,42)	39* (37,42)	40* (35,46)	35* (31,37)	38 (37,39)
Lemuriformes	50 (43,58)	50 (42,57)	62 (58,73)	66 (55,75)	59 (39,77)	50 (49,51)	46 (41,51)
Non-aye-aye lemurs	40 (33,48)	31 (27,35)	42 (35,50)	39 (33,46)	39 (26,50)	32 (27,37)	32 (29,34)
Archaeolemuridae	27 (20,33)	24 (20,28)	-	-	-	-	-
Palaeopropithecidae	23 (17,29)	21 (17,24)	-	-	-	-	-
Indriidae	21 (15,26)	17 (14,20)	39	36	17 (10,26)	18 (12,26)	21 (17,25)
Lemuridae	25 (19,32)	19 (16,22)	32 (26,39)	23 (19,29)	26 (16,37)	21 (15,26)	21 (18,25)
Lepilemuridae	16 (12,21)	12 (9,15)	37-38	32 (26,38)	12 (6,17)	9 (6,13)	16 (13,19)
Cheirogaleidae	30 (24,37)	25 (21,30)	29 (23,36)	23 (19,28)	25 (15,35)	22 (17,27)	24 (20,27)

Figure 2.3.
Simplified phylogeny of study taxa illustrating the systematics referred to in the text and the relationships of fossil taxa (indicated with crosses).

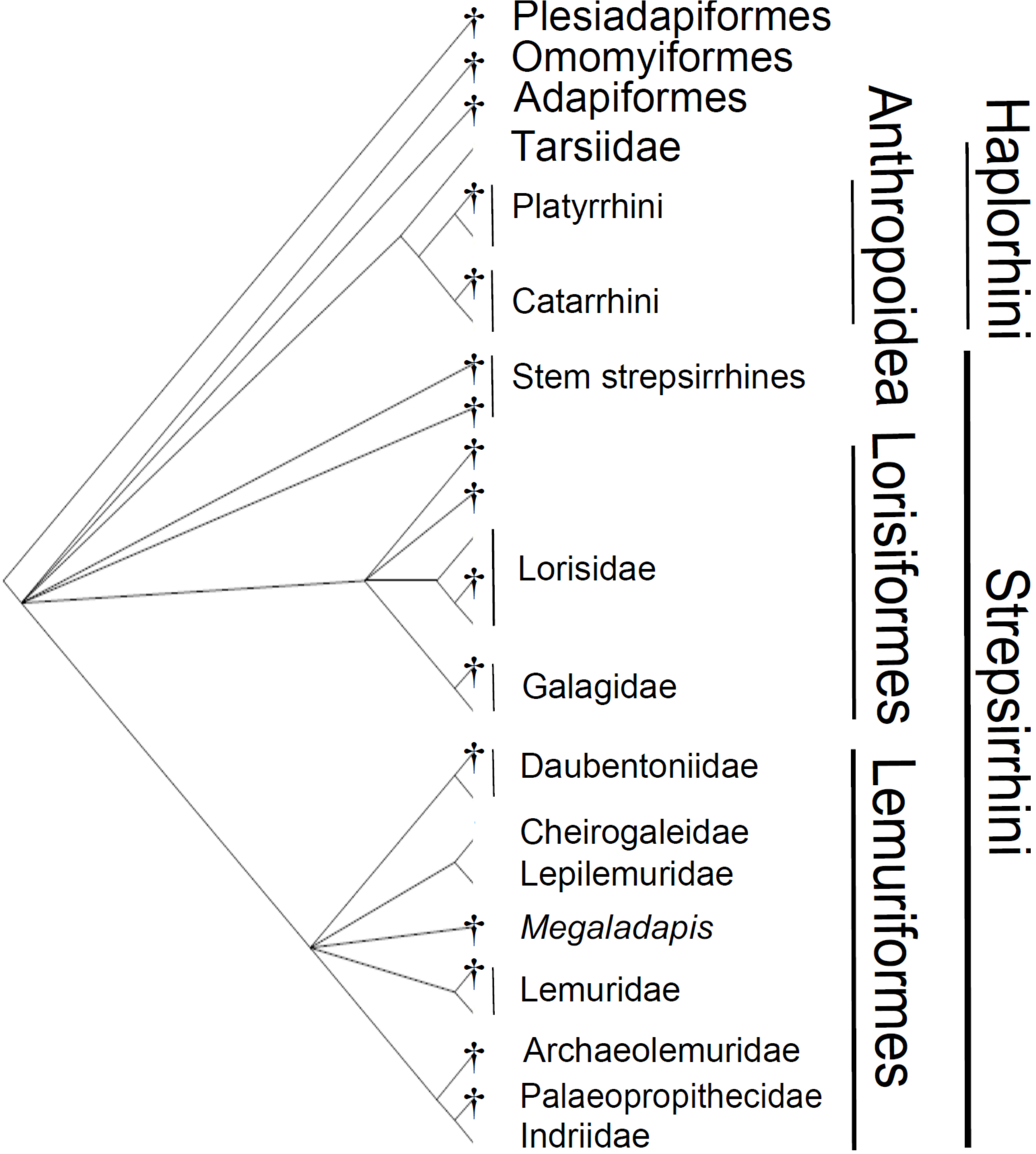


Figure 2.4.
Schematic of the study workflow illustrating data used, data processing procedures, and analytical techniques.

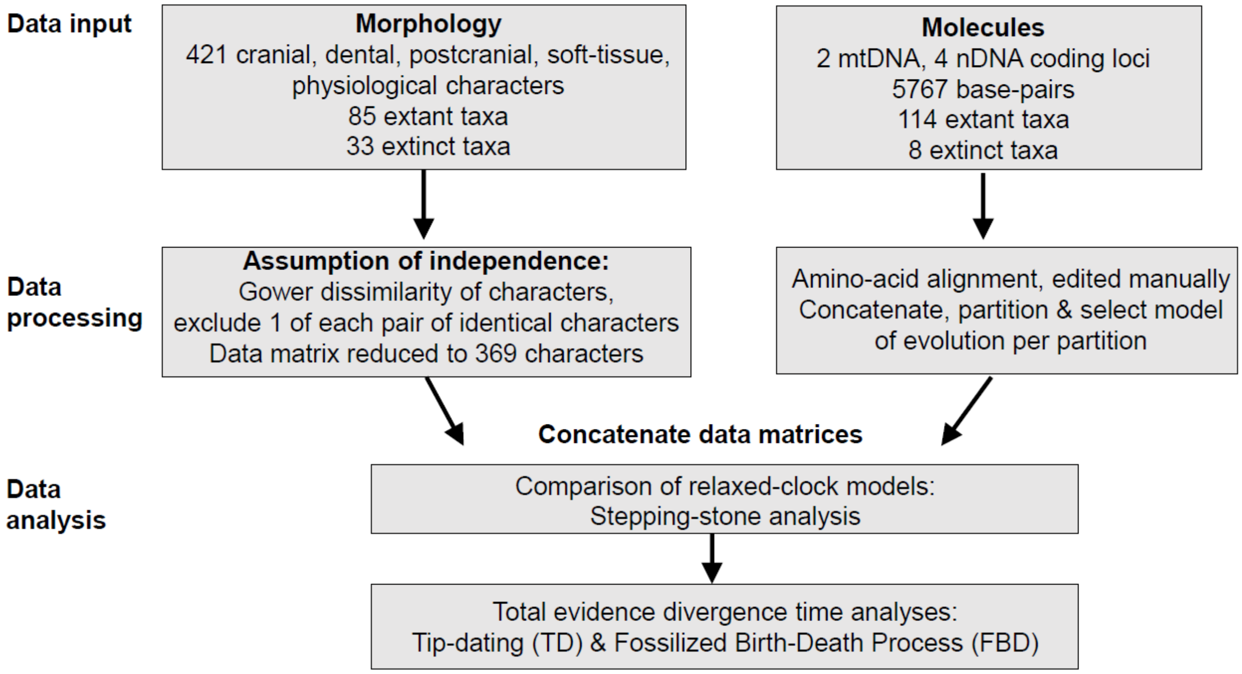


Figure 2.3.
Time-calibrated maximum clade credibility phylogeny inferred from a total evidence dataset (369 morphological, 5767 protein coding molecular characters). Divergence time estimates are based on the fossilized birth-death process (FBD). Node supports are illustrated with color coding, and nodes with no circles have posterior probabilities greater than 0.90, indicating strong support. The family names for monophyletic clades are given with illustrations of representative taxa. Of the taxa illustrated, representatives of the extinct subfossils are shown for each family. Illustrations of extant taxa from Schwitzer et al. 2013, extinct subfossils are from Mittermeier et al. 2010. Illustrations copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group. Used with permission.

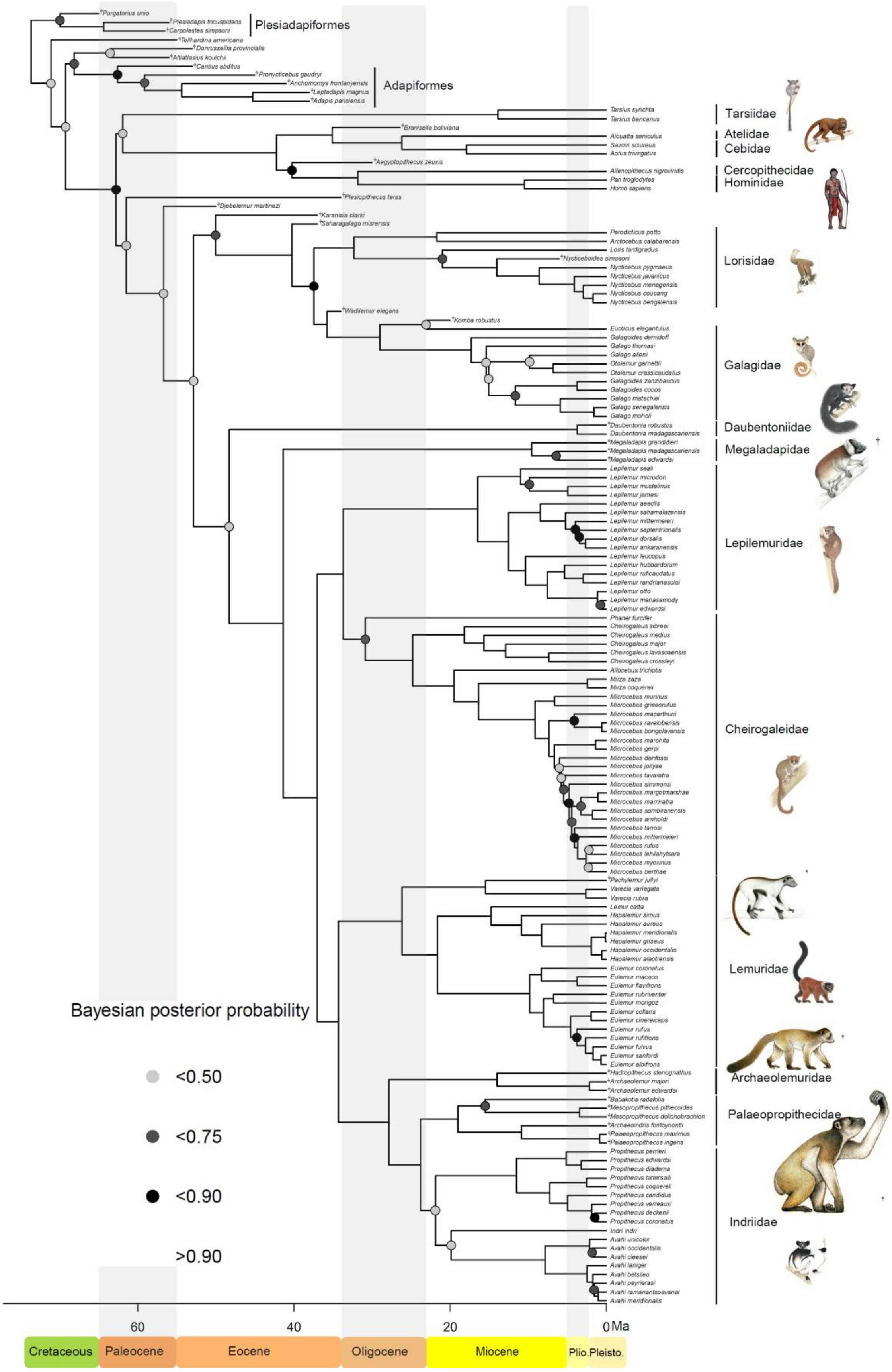
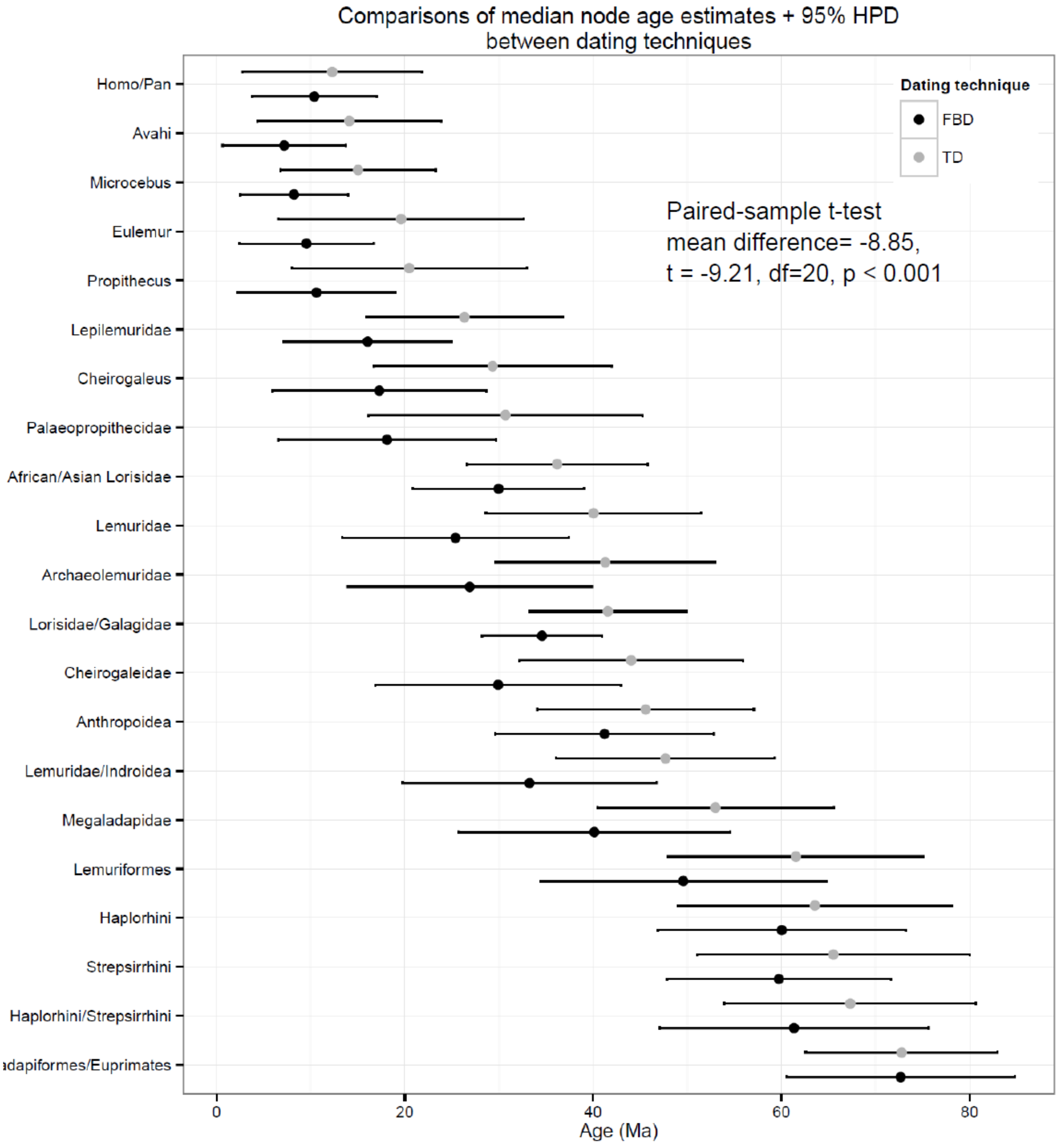

†Purgatorius unio
†Plesiadapis tricuspidens
†Carpolestes simpsoni
Plesiadapiformes
†Teilhardina americana
†Donrussellia provincialis
†Altiatlasius koulchii
†Cantius abditus
†Pronycticebus gaudryi
†Anchomomys frontanyensis
†Leptadapis magnus
†Adapis parisiensis
Adapiformes
Tarsius syrichta
Tarsius bancanus
Tarsiidae
†Branisella boliviana
Alouatta seniculus
Atelidae
Saimiri sciureus
Aotus trivirgatus
Cebidae
†Aegyptopithecus zeuxis
Allenopithecus nigroviridis
Cercopithecidae
Pan troglodytes
Homo sapiens
Hominidae
†Plesiopithecus teras
†Djebelemur martinezi
†Karanisia clarki
†Saharagalago misrensis
Perodicticus potto
Arctocebus calabarensis
Loris tardigradus
†Nycticeboides simpsoni
Nycticebus pygmaeus
Nycticebus javanicus
Nycticebus menagensis
Nycticebus coucang
Nycticebus bengalensis
Lorisidae
†Wadilemur elegans
†Komba robustus
Euoticus elegantulus
Galagoides demidoff
Galago thomasi
Galago alleni
Otolemur garnettii
Otolemur crassicaudatus
Galagoides zanzibaricus
Galagoides cocos
Galago matschiei
Galago senegalensis
Galago moholi
Galagidae
†Daubentonia robustus
Daubentonia madagascariensis
Daubentoniidae
†Megaladapis grandidieri
†Megaladapis madagascariensis
†Megaladapis edwardsi
Megaladapidae
†
Lepilemur seali
Lepilemur microdon
Lepilemur mustelinus
Lepilemur jamesi
Lepilemur aeeclis
Lepilemur sahamalazensis
Lepilemur mittermeieri
Lepilemur septentrionalis
Lepilemur dorsalis
Lepilemur ankaranensis
Lepilemur leucopus
Lepilemur hubbardorum
Lepilemur ruficaudatus
Lepilemur randrianasoloi
Lepilemur otto
Lepilemur manasamody
Lepilemur edwardsi
Lepilemuridae
Phaner furcifer
Cheirogaleus sibreei
Cheirogaleus medius
Cheirogaleus major
Cheirogaleus lavasoaensis
Cheirogaleus crossleyi
Allocebus trichotis
Mirza zaza
Mirza coquereli
Microcebus murinus
Microcebus griseorufus
Microcebus macarthurii
Microcebus ravelobensis
Microcebus bongolavensis
Microcebus marohita
Microcebus gerpi
Microcebus danfossi
Microcebus jollyae
Microcebus tavaratra
Microcebus simmonsi
Microcebus margotmarshae
Microcebus mamiratra
Microcebus sambiranensis
Microcebus arnholdi
Microcebus tanosi
Microcebus mittermeieri
Microcebus rufus
Microcebus lehilahytsara
Microcebus myoxinus
Microcebus berthae
Cheirogaleidae
†Pachylemur jullyi
Varecia variegata
Varecia rubra
Lemur catta
Hapalemur simus
Hapalemur aureus
Hapalemur meridionalis
Hapalemur griseus
Hapalemur occidentalis
Hapalemur alaotrensis
Eulemur coronatus
Eulemur macaco
Eulemur flavifrons
Eulemur rubriventer
Eulemur mongoz
Eulemur collaris
Eulemur cinereiceps
Eulemur rufus
Eulemur rufifrons
Eulemur fulvus
Eulemur sanfordi
Eulemur albifrons
Lemuridae
†
†Hadropithecus stenognathus
†Archaeolemur majori
†Archaeolemur edwardsi
Archaeolemuridae
†
†Babakotia radafolia
†Mesopropithecus pithecoides
†Mesopropithecus dolichobrachion
†Archaeoindris fontoynontii
†Palaeopropithecus maximus
†Palaeopropithecus ingens
Palaeopropithecidae
†
Propithecus perrieri
Propithecus edwardsi
Propithecus diadema
Propithecus tattersalli
Propithecus coquereli
Propithecus candidus
Propithecus verreauxi
Propithecus deckenii
Propithecus coronatus
Indri indri
Avahi unicolor
Avahi occidentalis
Avahi cleesei
Avahi laniger
Avahi betsileo
Avahi peyrierasi
Avahi ramanantsoavanai
Avahi meridionalis
Indriidae
Bayesian posterior probability
● <0.50
● <0.75
● <0.90
>0.90
60
40
20
0 Ma
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Plio.
Pleisto.

Figure 2.4.
Comparison of divergence-time estimates from two techniques used in this study, the Tip-Dating (TD) and the Fossilized Birth-Death Process (FBD) methods. Circles indicate the median age estimate and bars encompass the 95% highest probability distribution (HPD). Nodes are referred to by taxonomic names as in figures 1 and 3. The two methods differ significantly in the divergence time estimates for key nodes in the phylogeny, with the TD method estimating ages that are ~9 million years older than the FBD method, on average (paired-sample t-test, $p < 0.001$).



CHAPTER THREE

Increasing lineage diversification and decreasing phenotypic change through time in the lemurs of Madagascar

Abstract

The ecological limits hypothesis posits that an environmental carrying capacity sets an upper limit on species richness. Adaptive radiation theory predicts that by exploiting unique ecological opportunities, organisms escape the diversity limit and undergo rapid lineage and phenotypic diversification as they fill new adaptive zones. The diverse, endemic primates of Madagascar, called lemurs, have long been hypothesized to be an adaptive radiation. I tested the following predictions using phylogeny-based inferences: 1) lineage and phenotypic diversification exhibited an "early burst" of rapid diversification followed by decelerating rates, 2) lineage and phenotypic diversification were greater in lemurs than their sister clade in Africa and Asia (lorisiforms), and 3) optimal lemur body mass diverged in different adaptive zones of diet and activity. I inferred lineage-specific rates of diversification and phenotypic evolution, testing for topological and temporal rate shifts on a near-complete phylogeny of living and extinct lemurs (88%) and extant lorisiforms (68%). As predicted from adaptive radiation theory, lemur lineage diversification rate increased rapidly after colonizing Madagascar, while lorisiform diversification was constant through time. No significant shift in lineage diversification dynamics was observed between lemurs and lorisiforms, however. Counter to the ecological limits hypothesis, rates continued to increase to the present. Lemur body mass evolutionary rate was highest after colonizing Madagascar and declined toward the present, while in lorisiforms, the rate was low and constant over time. The optimal body mass and the rate of body mass evolution differed among diet and activity pattern adaptive zones, suggesting phenotypic evolution was adaptive. Increasing lineage diversification through time in lemurs was counter to

the ecological limits hypothesis, suggesting that lemurs did not reach a diversity equilibrium and other factors, such as biogeography, are related to increasing speciation.

Keywords: phylogenetic comparative methods, early-burst, subfossils, Bayesian Analysis of Mixture Models, Ornstein-Uhlenbeck, Strepsirrhini

Introduction

Macroevolutionary processes are tied to ecological processes at multiple geographic and temporal scales. The ecological limits hypothesis posits that species diversity is limited by a carrying capacity, determined by resource availability, leading to predictable patterns of evolutionary mode and tempo (Rabosky and Hurlbert 2015). One prediction of the ecological limits hypothesis is that as species diversity increases towards the carrying capacity, the rate of speciation should decrease and/or the rate of extinction should increase, leading to a diversity equilibrium (Rabosky 2009). Diversity equilibria can change, as exemplified by mass extinction events (Rabosky and Hurlbert 2015). Adaptive radiations perturb equilibrium dynamics by changing the carrying capacity for species able to exploit unique ecological opportunities; for example, invading a new habitat, lake, or island and diversifying due to open niches and competitive release (Schluter 2000a; Schluter 2000b; Seehausen 2006a). Speciation rates are predicted to be higher in clades that exploit ecological opportunity than in closely related clades which have not had the same ecological opportunity (Glor 2010; Schluter 2000b).

Adaptive radiation

In an adaptive radiation, organisms exploiting unique ecological opportunities are predicted to undergo rapid lineage and phenotypic diversification as they fill new adaptive zones (Gavrilets and Losos 2009; Glor 2010; Schluter 2000b). The rates of speciation and phenotypic diversification should be highest at the onset of the radiation, when species are diverging to fill unique niches (the “early burst” pattern, Ingram et al. 2012; Simpson 1944). As species accumulate and niches fill, the ecological limits hypothesis predicts that speciation and phenotypic diversification rates should decelerate and a new equilibrium is reached (Gavrilets and Losos 2009; Rabosky 2009; Rabosky and Hurlbert 2015; Schluter 2000b). Alternative explanations for decelerating diversification rates include non-adaptive speciation, such as repeated vicariance events which cause the splitting of fewer and fewer species with each event (Moen and Morlon 2014). Decelerating speciation and phenotypic diversification rates are observed in some adaptive radiations (McGuire et al. 2014; Reddy et al. 2012), but factors such as climate change, biogeography, and Red Queen effects also shape the curves of diversification rates through time (Fritz et al. 2012; Liow et al. 2011; Ricklefs 2010). In phylogeny-based inferences of diversification dynamics, the signal of an early burst in diversification will erode over geological time as species turnover leads to a concentration of nodes closer to the present (Rabosky and Hurlbert 2015). Testing these predictions in nature can clarify the roles of different evolutionary processes generating biodiversity.

Famous examples of adaptive radiations include *Anolis* lizards in the Caribbean (Losos 2009), Darwin’s finches of the Galapagos (Grant and Grant 2006; Lack 1947), and Lake Tanganyika cichlids (Seehausen 2006). These radiations are relatively recent in geological time (< 10 Ma) and concentrated in small geographic areas (islands or lakes). Madagascar, the fourth largest island in the world, has been isolated for more than 90 Ma, during which time relatively few clades could colonize the island (Samonds et al. 2013). Many of those clades that did arrive exhibit signals of adaptive radiation. The vangas, for example, had rapid early lineage diversification followed by a deceleration in diversification rate, concomitant with niche divergence followed by stasis (Reddy et al. 2012).

Lemurs of Madagascar

The primates of Madagascar, the endemic lemurs, have long been suggested to be an example of adaptive radiation (Martin 1972; Tattersall 1982). Living lemurs are taxonomically rich (99 species currently recognized, Schwitzer et al. 2013), in addition to 17 species of lemurs that have gone extinct within the last 2000 years (Godfrey et al. 2010). Living lemurs span a range of body sizes from the smallest living primates (30 g *Microcebus*) to around 10 kg, while some recently extinct taxa were as large as the largest living primate (up to 200 kg). There are diurnal and nocturnal species, frugivores and folivores, dry and wet forest species, and 10 to 14 species live in sympatry with discrete niches (e.g., Ganzhorn 1988).

Lemur species and ecological diversity are even more striking in comparison to closely related primates on the mainland. Lemurs belong to the clade Stresirrhini, and strepsirrhines in Africa and Asia (lorises and galagos) are mostly small, nocturnal omnivores represented by fewer species than lemurs (but see Pozzi et al. 2014). The dominant extant primates on the mainland belong to Haplorhini, the apes and monkeys, which came to dominate primate communities in the Oligocene and Miocene (e.g., Seiffert 2007). A long-standing hypothesis explaining the remarkable diversity of lemurs is that they evolved on Madagascar in isolation from other primates, and so they lacked the competition from haplorhines that may have suppressed the diversification of lorisiforms (Martin 1972; Tattersall 1982). Lemurs have niches similar to haplorhines on other continents (Fleagle and Reed 1996), even including ‘monkey-lemurs’ (Jungers et al. 2008). These patterns led early researchers to suggest that a generalized, nocturnal strepsirrhine ancestor dispersed to Madagascar and diversified to fill open niches via adaptive radiation (Martin 1972; Martin 2000).

The hypothesis that lemurs evolved via adaptive radiation has not been tested empirically. The predictions of adaptive radiation theory for speciation and phenotypic evolution can be tested in the framework of the phylogeny (Felsenstein 1985; Nunn 2011; O'Meara 2012). Inferences of the lemur phylogeny have improved dramatically with the increasing availability of molecular sequences and new phylogenetic inference techniques (Horvath et al. 2008; Perelman et al. 2011; Springer et al. 2012; Yoder and Yang 2000; Yoder 1994). Molecular analyses conflict, however, regarding the placement of major clades, including the earliest diversification of families characterized by short internodes and long branches (Horvath et al. 2008). Another impediment to studying the mode and tempo of lemur evolution is that there is no deep-time fossil record of lemurs on Madagascar, and Holocene subfossil lemurs are so derived they cannot be assumed to represent ancestral states (Godfrey and Jungers 2003). The extinct giant lemurs have been placed in the phylogeny based on the morphometric affinities of the extinct lemurs to living species (Jungers et al. 1997; Jungers et al. 1991), with many relationships supported by ancient DNA (Karanth et al. 2005; Kistler et al. 2015; Orlando et al. 2008). The molecular and morphological data for living and extinct lemurs had never been combined in a total evidence dating analysis until recently (Chapter Two). The total evidence approach enabled us to include all the available data and nearly all taxa (88% of lemurs) in the tree, and date the tree using dozens of fossil calibrations that were actually in the tree. A complete phylogeny is ideal for studying trait evolution and diversification because missing species bias the inferences of evolutionary events (Cusimano et al. 2012). Innovations in macroevolutionary techniques for estimating speciation, extinction, and phenotypic evolutionary rates have made it possible to test alternative hypotheses of changes in rates among lineages and through time (Figure 3.1, Alfaro et al. 2009; Rabosky 2014; Rabosky and Lovette 2008). It is now possible to test the adaptive radiation hypotheses for lemurs in ways that were never possible before.

Predictions of adaptive radiation theory for lemurs

I tested if lemur species and phenotypic diversity have evolved via adaptive radiation. Based on the ecological theory of adaptive radiation and the ecological limits hypothesis as outlined above, I make the following predictions for lemurs.

1) If lemurs diversified via an adaptive radiation, then lineage diversification rates increased rapidly after lemurs colonized Madagascar. In contrast, if lemurs reached an equilibrium early then they exhibit a constant diversification rate near zero. If recent events led to high species richness, then lemurs had increasing diversification rates towards the present, rather than an “early burst”.
2) If lineage accumulation was limited by ecological bounds, then lineage net diversification rates (speciation – extinction) declined over time and approach zero as an equilibrium is reached. If diversification was promoted by recent events, then lineage diversification increased towards the present.
3) If lemurs had ecological opportunity that closely related strepsirrhines on the mainland, lorisiforms, did not, then lineage diversification was higher in lemurs than in closely the lorisiforms. In contrast, if the difference in species numbers can be attributed to the relatively younger crown-group age of lorisiformes than lemurs, then diversification rates in lemurs were not higher than those in close relatives.
4) Concurrent with speciation rates, the rate of lemur phenotypic evolution was highest after colonization and decelerated towards the present. In contrast, if environmental or

developmental constraints prevented phenotypic diversification, a constant or gradual rate of phenotypic evolution is predicted.

5) If lemurs are an adaptive radiation, then lemur phenotypic evolutionary rates are predicted to be higher than in the closely related lorisiforms. If lemur phenotypes were constrained developmentally then they are not predicted to differ in phenotypic evolutionary rates from lorisiforms.
6) If lemurs evolved via adaptive radiation, then lemur phenotypes are predicted to have diverged in relation to shifts in adaptive zones of diet and activity pattern. Optimal phenotypes, rates of evolution, and evolutionary constraints differ among niches. If lemur phenotypic evolution was constrained by other adaptive forces, then phenotypes do not differ markedly among adaptive zones.

Materials & Methods

Testing for adaptive radiation

To test if lemurs diversified via an adaptive radiation, my analyses aim to 1) estimate the lineage-specific speciation and extinction rates to quantify net diversification and identify shifts in diversification rates through time and across the tree, 2) estimate the rate of phenotypic evolution through time and identify shifts in phenotypic evolution, 3) test the link between body mass (phenotypic trait), diet and activity pattern (adaptive zones) and test for different phenotypic optima in different niche regimes.

Taxonomic sampling and phylogeny

The taxonomy of lemurs has changed recently with the increase in available molecular evidence suggesting many cryptic species that were previously subsumed as single species. I recently inferred a near-complete phylogeny that includes 87 living lemurs (87.9% out of 99 recognized taxa, Mittermeier et al. 2010, Schwitzer et al. 2013) and 14 extinct subfossils (82.4%, Godfrey et al. 2010). I compared speciation and phenotypic evolutionary rates between lemurs and extant lorisiforms (lorises and galagos) of Africa and Asia (67.9%, 19 / 28 IUCN recognized species). I accounted for incomplete species sampling in lineage diversification analyses by specifying the proportion of sampled species for each genus (Pybus and Harvey 2000; Rabosky 2014, Appendix II). To investigate the effects of incomplete sampling, complete trees and traits were simulated with known lineage and phenotypic diversification parameters, subsampling tips as in the empirical dataset. The observed lineage diversification rate estimates were robust to incomplete sampling, the distributions of phenotypic rate estimates with full and subsampled datasets overlapped each other and the true value, and traits simulated under a single rate model were not inferred to have evolved under a model of multiple rates due to incomplete sampling (Appendix II). In the comparative analyses described below, I used the maximum clade credibility (MCC) phylogeny inferred from total evidence analysis under the fossilized birth-death process model, as well as two variants to evaluate if the results are robust to changes in the phylogenetic relationships. 1) An alternate topological hypothesis with the genus *Megaladapis* sister to the family Lemuridae, as supported by recent studies of ancient mitochondrial DNA (Kistler et al. 2015, Karanth et al. 2005, Orlando et al. 2005). I extracted and grafted *Megaladapis* with the placement and the estimated divergence times proposed from previous studies. 2) The MCC tree of only extant lemurs to evaluate the effects of observed extinctions on the estimates of diversification dynamics.

Trait data & phylogenetic comparative methods

In testing for adaptive patterns of niche evolution, it is necessary to identify ecologically relevant traits (Freckleton 2009). I chose body mass as a phenotypic trait related to discrete adaptive zones of diet and activity pattern. Body mass is well known to be related to many aspects of a species' physiology, life history, and ecology, thus encompassing much of the biology of the organism (Cooper and Purvis 2010; Price and Hopkins 2015). Body mass is tightly correlated to diet, but there are many adaptations to diets beyond changes in body mass (e.g., gut morphology, resource extraction strategy) that lead to deviations from the correlation of diet and body mass. Diet and activity pattern are important variable defining a species' niche, with many morphological and physiological correlates, and which influence interspecies competition.

To gather the phenotypic and niche data, I searched primary literature sources (Appendix II). I obtained body mass estimates for 116 species, and despite the species sampling being incomplete, body mass data were obtained for species representing the full range of variation for lemurs (smallest: *Microcebus berthae* = 30 g, largest extant: *Indri indri* = 6500 g, largest extinct: *Archaeoindris fontoynontii* = 161200 g) and lorisiforms (smallest: *Galagoides demidoff* = 61 g, largest: *Otolemur crassicaudatus* 1150 g). Body mass was natural log transformed for further analyses. All taxa were grouped into two dietary categories: folivore or omnivore. Folivores were species whose primary dietary adaptations are for consuming leaves, with leaves typically making up >50% of the diet (e.g., species with sharp and sheering crests on molars, enlarged caecum for hind-gut fermentation, Fleagle 2011). Omnivores were species whose primary diet included a combination of fruit, insects, exudates, and/or nectar. These coarse categories do not reflect the proportions of food types in the diet; some species eat a considerable amount of fruit or seeds (*Propithecus* species), but their primary dietary adaptations and highest proportion of dietary intake is folivory; thus they were coded as folivores. These data were taken from the literature and grouped based on interpretations of the dietary niches of the organisms (Baab et al. 2014; Campbell et al. 2010; Gómez and Verdú 2012; Hartwig 2002). For extinct taxa, the morphology of the dentition has been the primary source of dietary inference (Boyer 2008; Godfrey et al. 2012; Kay 1975; Kay and Covert 1984). I categorized species as either diurnal or nocturnal based on their primary activity period. I grouped cathemeral species into the diurnal category because within lemurs, cathemerality has only evolved in one clade, Lemuridae, documented primarily in *Eulemur* and *Lemur catta*, with anecdotal evidence of some nocturnal activity in other lemurids (LaFleur et al. 2014; Parga 2011; Tattersall 2008; Wright 1999). This limits the power of comparative analyses to test patterns related to cathemerality (Maddison and FitzJohn 2015). Further, while some lemurs are known to be cathemeral with frequent bouts of activity at night, their predominant activity is diurnal, and for many species their cathemeral activities are seasonal, related to moonlight, or contentious (Curtis and Rasmussen 2006; Curtis 2007; Kappeler and Erkert 2003). In a broader taxonomic sample including all primates, a relationship was shown between activity pattern (including cathemerality), and diversification rates (Santini et al. 2015). Finally, each taxon was assigned a categorical niche state: nocturnal omnivore, diurnal omnivore, nocturnal folivore, diurnal folivore (see Appendix II for data with references).

Lineage and phenotypic diversification rates

To measure lineage and phenotypic diversification rates through time, I quantified the diversification dynamics of strepsirrhines using a Bayesian inference approach (Bayesian Analysis of Macroevolutionary Mixtures, BAMM, Rabosky 2014). The BAMM analysis specifically compares the probability of lineage and phenotypic diversification under constant time- and lineage-variant models to models including heterogeneity in rates among lineages. BAMM, like most phylogeny-based speciation and extinction models, assumes all observed tips survive to the present and therefore can only handle ultrametric trees (Maddison et al. 2007;

Pyron and Burbrink 2012; Rabosky 2014). To retain the subfossil lemurs, which are so important to test predictions about lineage and phenotypic evolutionary rates, I added the time since extinction to their branch lengths to bring those tips to the present. This is not expected to bias the analyses because the amount of evolutionary change expected within the last 1000 years since extinction is negligible compared to ~30-50 million years of evolutionary history.

To set prior parameter probabilities, for speciation and extinction rate analyses I used a rate shift Poisson parameter prior of 1, which places the highest probability on fewer rate shifts and is appropriate for small trees (Rabosky 2014). Other priors were adjusted empirically based on the trees using the *BAMMtools* package (Rabosky et al. 2014) in the R statistical environment (R Core Team 2014). For the speciation and extinction rate analyses, these were lambda (speciation rate) = 2.7 – 2.8, lambda shift prior (probability of a shift in speciation rates) = 0.02, extinction prior = 2.7 – 2.8. For the phenotypic analysis of the body mass dataset, I used default priors with the trait range prior based on a uniform distribution from the range of the observed data, Poisson rate prior = 1.0, and beta shift prior (probability of a shift in trait rate) = 0.05. The prior values in the lineage and phenotypic analyses place the highest probability on fewer rate shifts; in fact, the null model is no shift. The advantage of the BAMM analysis is that, because BAMM samples rate shift models using a reversible jump Markov Chain Monte Carlo algorithm, the probability of the model (marginal likelihood) with one or more rate shifts can be compared to the probability of the model with no rate shifts using Bayes factor ratios (marginal likelihood of a model with a shift / likelihood of a model with no shift). This technique enables comparisons of the probability and location of rate shifts in the tree based on the prior probability of a shift, which is determined by branch lengths. Further, the branch-specific posterior probability of a shift can be compared to the branch-specific prior probability because the prior is based on the branch length. High species richness in a clade with relatively short branches would be inferred to have a greater probability of a rate shift than expected under the prior. Bayes factor ratios > 3 suggested support for the alternative model (Kass and Raftery 1995). The probabilities of the time-variable and time-invariant models were compared using Bayes factor ratios.

I ran the BAMM analysis for 100 million generations, recording parameters every 5000 generations and determined convergence by plotting the model likelihoods by generations and calculating the effective sample size values in the *coda* package (Plummer et al. 2006) for R. Histograms of the posterior distribution of diversification rate estimates at the lemur and loris nodes were compared to determine if diversification rates differed between the two lineages. Branch-specific shift probabilities were evaluated using Bayes factor ratios of the posterior probability of rate shifts on each branch to the prior probability of a shift expected given the branch lengths. I obtained and plotted estimates of lineage and phenotypic diversification rates through time using the *getRateThroughTimeMatrix* function in *BAMMtools*.

Phenotypic evolutionary optima

To test the adaptive relationship between phenotype and niche divergence, I tested the hypothesis that adaptive zones have different phenotypic optima and evolutionary rates. I inferred the location of combined diet and activity adaptive zones on the phylogeny by first inferring ancestral states at nodes using a maximum-likelihood method for discrete traits, which uses the subtree-pruning algorithm to estimate the marginal likelihood of ancestral states [*rerootingMethod* function implemented in the *phytools* package (Revell 2012) and *fitDiscrete* function in *Geiger* (Harmon et al. 2008) for R]. I compared the fit of the discrete trait evolution inferences under equal, symmetrical, and asymmetrical rates Mk models and selected the best model based on the lowest score of the Akaike Information Criterion corrected for small sample size (AICc). The most likely state at each node was extracted and mapped onto the nodes for subsequent analysis. I then tested the fit of the following models of body mass evolution in relation to the evolution of adaptive zones: 1) one Brownian Motion model (BM) fits for the whole tree, 2) one adaptive peak model (OU) fits for the whole tree, 3) one unique BM model for each niche regime, each with its own variance, 4) one unique OU for each regime, each with its own optimal mean, 5) same as 4 but with unique variance (σ^2) parameters for each regime [implemented in the *OUwie* package (Beaulieu et al. 2012) in R]. I did not rescale the tree for this analysis, such that units are in the original time scale, and the root state was estimated from the model, which in the *OUwie* implementation is assumed to be the stationary distribution of the model.

Results

Lineage diversification rate

The MCMC chains exhibited convergence and stationarity after 0.5 million generations, earlier samples were discarded as burn-in, and post-burn-in ESS values were high (>1500), confirming adequate sampling of the posterior distribution. Across topologies, the overall results were the same, quantitative differences were slight, and here I focus on the results with the original MCC tree (see Appendix II for results with other topologies).

Prediction 1: increasing lineage diversification rate early in lemur evolution: The diversification rate estimates through time suggest that rates increased most rapidly early in lemur evolution (Figure 3.2). Rates were low initially (~0.04 lineages / million years ago, Ma, at 50 Ma) and increased rapidly to ~ 0.06 lineages / Ma by 40 Ma. The magnitude of the increase in the rate through time decreased gradually, suggesting the speciation rates were highest after colonizing Madagascar.

Prediction 2: decreasing diversification rates through time: Counter to the predictions of the ecological limits hypothesis, I found no evidence of decelerating diversification rates in either lemurs or lorisiforms. Instead, the diversification rates of lemurs increased early after colonization and then remained relatively constant with positive rates while lorisiforms had constant positive rates, suggesting recent causes of positive diversification (Figure 3.2).

Prediction 3: higher diversification rates in lemurs than in lorisiforms: Lorisiform lineage diversification rates were approximately constant through time and overlapped with the rate estimates for lemurs (Figure 3.2). If diversification dynamics differed between lemurs and lorisiforms, a rate shift was predicted. Counter to this prediction, the null model of no rate shifts had the highest posterior probability (0.56), with the second highest probability for one shift (0.32) and low probabilities (<0.10) for more shifts. Based on the Bayes factor ratios of the marginal probability of the null model (no shifts) to models with one or more shifts, there is little support for rejecting the null hypothesis of no shifts (BF ratio ~0.86 and ~0.49 for the alternate models of one and two rate shifts compared to the null, respectively Kass and Raftery 1995). Comparing branch-specific posterior probabilities of a speciation-extinction rate shift on a branch with the prior probability of a shift based on branch lengths with Bayes factors, branches with evidence of a shift include those leading to the genera *Microcebus* and *Avahi*, which had higher probabilities of a shift to higher diversification rates than expected under the prior given its short branches (BF ratio = 20-69 for branches leading to and within *Microcebus* and *Avahi*). To further illustrate the diversification dynamics on the tree, histograms of the posterior distribution of speciation or net diversification rates between lemurs and lorisiforms as well as among genera of lemurs suggests there were no differences among lineages, and that diversification rates in lemurs have been increasing through time in all lineages (Appendix II).

Body mass evolutionary rate

Prediction 4: highest phenotypic evolutionary rates early in lemur divergence: The BAMM phenotypic rate analysis showed strong signs of convergence with stable likelihood values achieved by 0.5 million generations, and ESS values >1000. Plotting the phenotypic evolutionary rates through time illustrates that phenotypic rate was highest early in lemur diversification, followed by a decline in rates towards the present (Figure 3.2).

Prediction 5: higher phenotypic evolutionary rates in lemurs than in lorisiforms: The posterior probability of rate homogeneity across the tree is low (0.01) compared to the posterior probability of one (0.52) or two (0.26) rate shifts. Bayes factor comparison suggests there is strong support for one rate shift compared to the probability of no shifts (BF ratio = 195), and no support for two shifts compared to one (BF ratio = 0.80). Comparing the branch-specific posterior probability of a shift to the prior probabilities, there is strong evidence for a rate shift on the branch after the divergence of *Daubentonia* from all other lineages (Appendix II). Body mass evolutionary rate was highest early in lemur diversification, and decreased towards the tips for all lineages except *Daubentonia*, the sister lineage of all other lemurs, which had a higher rate near the tips than other lineages (Figure 3.3). This result is driven by the divergent body masses between the extant *D. madagascariensis* (~2kg) and the extinct *D. robustus* (~10kg) coupled with the short branches separating them (divergence ~3 Ma). In contrast, the lorises and galagos of Africa exhibited a low and relatively constant rate of phenotypic evolution.

Phenotypic optima in different adaptive zones

Prediction 6: divergence in phenotypes related to adaptive zones: The likelihood of ancestral state estimates for diet and activity niche were similar between an equal transition rate model and a symmetrical model (AICc = 64.25 vs 64.32) and the asymmetrical rates model had low support

(AICc = 79.77); thus, I retained the equal-rates model results because addition of constraints on transition probabilities does not improve the model. I inferred the most likely ancestral states of each node onto the phylogeny to specify the location of niche regimes for the OUwie analysis (Figure 3.3). The models that fit the data best are state-dependent OU models with unique mean optimum body masses and evolutionary variance parameters (σ^2) for each category and the same α parameter value across states (Table 3.1). Alpha values were low (<0.001) and when interpreted as phylogenetic half-life ($\ln(2)/\alpha$, Hansen et al. 2008), the time to reach the optima was greater than the length of the phylogeny, suggesting the evolutionary constraint around optima was low. The mean optimum for diet categories suggested larger body sizes were optimal for diurnal omnivores (mass = 26 kg, se = 2.97) and folivores (13 kg, se = 3.94), while smaller body size was optimal for nocturnal folivorous and omnivorous species (0.8kg, se=4.31; 0.4kg, se = 1.97, respectively). Evolutionary rate was slightly higher in diurnal folivores (σ^2 = 1.05 g/Ma) than in diurnal or nocturnal omnivores, and nocturnal folivores had a slower rate than other niche categories (1.005 g/Ma). In sum, these results suggest that lemurs radiated into unique diet and activity pattern niches, and each niche regime evolved towards unique optima, but at different rates across the tree.

Discussion

I found that lemur diversification dynamics only partially fit the predictions of the ecological theory of adaptive radiation. Further, lemur diversification does not exhibit the equilibrium dynamics predicted from the ecological limits hypothesis. The rate of lineage diversification in lemurs increased rapidly subsequent to the colonization of Madagascar, as expected in an adaptive radiation. Diversification rates never decreased or approached zero, however, as would be expected if a new equilibrium had been reached. Counter to predictions for an adaptive radiation, the lineage diversification rates of lorisiform primates did not differ from lemurs. The rate of lemur body mass evolution exhibited the predicted “early-burst” of high rates of change after colonization followed by declining rates towards the present. Lorisiforms, on the other hand, had constant, low rates of phenotypic evolution since the origin of their crown clade near the Eocene-Oligocene boundary. Concordant with the phenotypic adaptation predictions of adaptive radiation theory, body mass evolved at different rates and towards unique optima in each adaptive zone. My study tests the long-held assumption that lemurs are an adaptive radiation, and sheds light on the hypotheses of adaptive radiation and ecological limits that predict the dynamics of lineage and phenotypic diversification. From my results, I argue that lemur diversification has properties of an adaptive radiation early in their divergence from lorisiforms, but many factors have shaped diversification dynamics over their long evolutionary history. Further, while lorisiforms are not as species rich as lemurs, their diversification rates indicate that they have maintained positive rates since the divergence of the crown group.

Do lemur lineage and phenotypic diversification dynamics fit the predictions of the ecological theory of adaptive radiation?

I tested if lemur speciation and phenotypic evolutionary rates fit the predictions of an adaptive radiation. First, I tested if lemur lineage diversification was highest at the beginning of their evolution, as expected if new ecological opportunity sparks speciation (McGuire et al. 2014; Redding et al. 2010). I found that initial lineage diversification rates were low and increased most rapidly within the first 10 Ma of lemur divergence, followed by constant positive rates. There was also some support for a unique shift to higher diversification rates in the genus *Microcebus*, a recently diverged clade (~8 Ma) with more than 20 species.

The ecological limits hypothesis predicts that, in an adaptive radiation, the ability of organisms to exploit ecological opportunity causes an increase in the environmental carrying capacity (Rabosky and Hurlbert 2015). As species richness increases and the new carrying capacity is reached, diversification rates should decline. I found no evidence for declining diversification rates in lemurs or lorisiforms. The constant positive rates suggest other factors have maintained non-equilibrium dynamics in both groups, as discussed below.

I tested the prediction from adaptive radiation theory that lemur phenotypic evolution should exhibit a signature of an "early burst", followed by a decrease in rates towards the present. Rapid phenotypic divergence into open niches followed by a plateau in rates is a hallmark of adaptive radiations such as the anoles of the Greater Antilles (Losos 2010; Mahler et al. 2010) and African cichlids (Seehausen 2006b). Despite that the early-burst pattern of phenotypic evolution is rarely observed (Harmon et al. 2010), my results suggest there was a burst of rapid phenotypic (body mass) change related to niche diversification, with the highest rates of phenotypic evolution after the initial colonization of Madagascar, followed by decelerating rates towards the present. In contrast, the rate of phenotypic evolution in lorisiforms was relatively low and constant over time. This heterogeneity in evolutionary rates is consistent with the hypothesis that lemurs initially diverged on niche axes related to body size and subsequently retained those niches to the present.

For an evolutionary radiation to be considered adaptive, the phenotypic evolutionary dynamics must reflect adaptations to rapidly diverging niches (Gavrilets and Losos 2009; Glor 2010; Schluter 2000b). I found evidence of an adaptive relationship between body mass and diet/activity pattern adaptive zones, such that lineages evolved towards higher body mass optima in diurnal folivores and omnivores, while nocturnal folivores and omnivores evolved towards lower body mass optima. The results reflect the early diversification of clades into distinct diet and activity pattern niches, coupled with a slow subsequent evolution of body mass. The body mass evolutionary rate estimates differed among adaptive zones, suggesting the level of constraints on body mass evolution vary among niches. Body mass is strongly correlated to diet in mammals, such that herbivores are larger than insectivores because of the relative differences in energy demands and physiological adaptations to digestion (reviewed in Kay 1975; Müller et al. 2013; Price and Hopkins 2015). While many folivorous lemurs are large-bodied (including many of the giant extinct lemurs, Godfrey et al. 2012), three diverse clades of lemurs are small-bodied folivores (~1kg), and two of those are nocturnal. These small folivores have unique anatomical, physiological and behavioral adaptations to their low-nutrient diets (Faulkner and Lehman 2006; Ganzhorn et al. 1985; Ganzhorn 1988; Ganzhorn 1992; Perrin 2013; Tan 1999). These patterns are consistent with the hypothesis that initial divergences into adaptive zones were coupled with shifts in body size.

Why was there no shift in lineage diversification rates between lemurs and lorisiforms?

One prediction from the ecological theory of adaptive radiation is that clades which had unique ecological opportunities for diversification should have higher species richness as a result of higher diversification rates than clades that did not have the same ecological opportunities (Schluter 2000b). I found no evidence for a shift in the lineage diversification rates between lemurs and lorisiforms and the lorisiform rates overlapped the lemur rates since the divergence of the crown clade. The result suggests that the difference in species richness between lemurs and lorisiforms is not due to lower diversification in lorisiforms, but possibly due to the shorter time for speciation compared to lemurs.

Remarkably, lorisiform diversification rates were similar to those of lemurs, despite the three-fold difference in species richness between the two groups. Lorisiforms diverged near the Eocene-Oligocene boundary, a time of high extinction for stem strepsirrhines in Afro-Arabia, possibly due to colder, drier and/or more seasonal climates associated with Antarctic glaciation (Seiffert 2007). There are only three known fossil lorisiforms that are late-Eocene in age (37 – 34 Ma), inferred to be stem or crown lorisiforms (this dissertation, Chapter Two; Seiffert 2012). Around the same period, anthropoids became abundant in Africa and Asia. The ancestral lorisiforms may have maintained high diversification rates by filling the nocturnal niche previously occupied by many stem strepsirrhine competitors and avoiding competition with diurnal haplorhines. The paucity of fossil lemurs and stem lorisiforms precludes validation of hypotheses about extinction at present. Interpretations of extinction dynamics are limited in this study because estimates of extinction rates from extant datasets are underestimated (Quental and Marshall 2009; Rabosky 2010). The results presented here based only on extant taxa may be limited by the lack of diversity data along the stem lorisiform lineage, but suggest that some factor has maintained positive diversification rates in lorisiforms similar to the rates in lemurs.

Why was there no decline in lineage diversification rates?

The ecological limits hypothesis predicts that speciation rates decrease with increasing species richness as speciation and extinction rates reach a diversity-dependent equilibrium (Rabosky and Hurlbert 2015). I observed no decline in diversification rates in lemurs or lorisiforms, suggesting that either they have not reached a carrying capacity, even after 30 – 50 Ma, or that there are no ecological limits. There are many evolutionary mechanisms and methodological artifacts that can drive slow-downs in diversification rates (Moen and Morlon 2014; Quental and Marshall 2013; Rabosky 2009; Rabosky and Lovette 2008). Less attention has been paid to mechanisms causing increasing diversification rates through time, possibly because increasing rates are much less commonly observed (Brock et al. 2011).

Inferences of diversification rates are a time-slice in a continuum of changing speciation and extinction rates. Using simulations and a statistic of tree shape known as gamma (Pybus and Harvey 2000), it was shown that clades evolving under diversity-dependent speciation and constant extinction exhibited a pattern of nodes concentrated towards the past near the equilibrium point, but after longer time periods, extinction eroded the early burst signal and resulted in trees with nodes concentrated towards the tips (Rabosky and Hurlbert 2015). Given the long geological time scale of lemur evolution (~50-60 Ma), diversity may have reached an equilibrium long in the past, after which extinction pruned old lineages resulting in a tree structure with nodes concentrated towards the present. In defense of the argument that speciation rates have increased, the BAMM statistical framework estimates time- and lineage-varying speciation rates and a constant extinction rate empirically, and is more powerful for inferring evolutionary dynamics than the course tree-shape statistic gamma. More explicit simulations of varying extinction rates may be needed to verify the effects of extinction on net lineage diversification.

Evidence from paleontology, phylogenetic models, and community ecology refute equilibrium dynamics (Harmon and Harrison 2015). The lemur diversification rates illustrated that after colonization, diversification rates increased rapidly and remained positive until the present. Other factors that could explain prolonged positive diversification rates include biogeographic events. Geographic isolation and vicariance events lead to speciation (Coyne and Orr 2004), and vicariance due to the climate-driven fragmentation of suitable habitat can lead to spikes in diversification rates (Lovette and Bermingham 1999). In some cases, vicariance may lead to a slow-down in diversification rates as the repeated subdivision of ranges affects fewer and fewer species (Moen and Morlon 2014). In contrast, dispersal can lead to high speciation rates as lineages regularly encounter new ecological opportunities (Fritz et al. 2012; Moen and Morlon 2014). Lemurs most likely colonized Madagascar during a time when arid environments were gradually transitioning to moist tropical conditions as Madagascar drifted north of the Tropic of Capricorn in the Eocene (Samonds et al. 2013; Wells 2003). During this shift in climate, lemurs may have experienced increasing diversification rates as they adapted to new habitats. Global cooling and drying at the beginning of the Oligocene are hypothesized to drive the observed turnover in some primate assemblages, including the extinction of stem strepsirrhines at northern latitudes (Seiffert 2007). This global cooling event may have led to aridification of Madagascar and forest fragmentation with subsequent vicariance of allopatric populations. Vicariance and dispersal events related to the appearance of riverine dispersal barriers have been hypothesized to be important factors in the historical biogeography of lemurs as well (Ganzhorn et al. 2006; Pastorini et al. 2003; Yoder and Heckman 2006). These climatic and biogeographic factors may have led to positive lineage diversification rates in lemurs.

More complex explanations for the positive lineage diversification rates could involve a lack of steady-state between hosts and pathogens (Ricklefs 2010), predators and prey, and competition (e.g., Red Queen Hypothesis, Liow et al. 2011; Van Valen 1972). One example of a possible Red Queen effect that may have been related to increasing diversification rates through time is the late arrival of competitors and predators to Madagascar. The origins of mammalian carnivores on Madagascar is estimated ~ 20 – 30 Ma and large diurnal raptors ~ 10 Ma (Yoder and Nowak 2006). Lemurs had initially evolved with presumably few predators, and the arrival and diversification of carnivores and raptors may have triggered an evolutionary race between lemurs and their predators. Competition among lemur species for resources may also have driven increasing diversification as lemurs partitioned niches along different axes. For example, not only do co-occurring lemurs differ in coarse dietary categories (folivore or omnivore), but sympatric folivorous species select leaves with different secondary compounds (Ganzhorn 1988). Further investigation of the possible phenotypic, biogeographic, or ecological drivers of increasing diversity and diversification rates through time are required to clarify the findings reported here.

In conclusion, for the first time using empirical data I tested the hypothesis that the lemurs of Madagascar are an adaptive radiation. Lemurs had an increasing diversification rate early in their divergence from the lorisiforms on the mainland, but rates did not differ from lorisiforms. Counter to predictions from the ecological limits hypothesis, diversification rates showed no signs of declining. Lemur phenotypic divergence was highest early after the colonization of Madagascar as lineages diverged in adaptive zones of diet and activity pattern and declined quickly towards the present, while lorisiforms exhibited low and constant rates. These results suggest the initial divergence of lemurs was related to adaptive radiation, but over their long evolutionary history many factors have further shaped their diversity.

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Tables and figures

Table 3.1.
Summary of model comparison results for state-dependent Brownian Motion (BM) and Ornstein-Uhlenbeck (OU, OUwie package in R). In this analysis, the ancestral inferences for diet and activity pattern niches are mapped onto the tree as 'adaptive zones' from ancestral state estimations (rerootingMethod in R). Then, I compared the likelihood of overall models of phenotype evolution with the same parameters across the whole tree to regime-specific models in which each regime has its own evolutionary parameters. 'BM1' is equivalent to one BM model across the whole tree, and 'OU' is equivalent to one OU model. 'OUM' is a state dependent optimum model, and 'OUMV' is a state dependent optimum and variance model. Niche categories are as follows: Noct-Om: nocturnal omnivore, Diurn-Om: diurnal omnivore, Noct-Fol: nocturnal folivore, Diurn-Fol: diurnal folivore. The best-fitting model was an OU model with a single (weak) α parameter for all states and state-dependent evolutionary variances and mean optimal body masses. This indicates that each dietary regime has the optimum body mass and evolutionary rate indicated in the table.

Model	**Optimal means (se)**	**α**	**σ^2**	**LnL**	**AICc**	**AICw**
BM1	7.22 (0.56)	-	0.03	-82.63	169.36	<0.001
BMS	7.22 (0.64)	-	Noct-Om: 0.46 Diurn-Om: 0.03 Noct-Fol: 0.005 Diurn-Fol: 0.04	-70.29	151.16	0.25
OU1	7.22 (0.56)	1.0E-6	0.03	-82.63	171.25	<0.001
OUM	Noct-Om: 9.24 (1.25) Diurn-Om: 9.93 (1.18) Noct-Fol: 5.53 (1.76) Diurn-Fol: 6.32 (0.70)	1.0E-6	0.03	-77.18	167.16	<0.001
OUMV	Noct-Om: 9.50 (1.37) Diurn-Om: 10.19 (1.09) Noct-Fol: 6.70 (1.46) Diurn-Fol: 6.07 (0.69)	1.0E-6	Noct-Om: 0.05 Diurn-Om: 0.02 Noct-Fol:0.005 Diurn-Fol: 0.03	-64.58	148.95	0.75

Figure 3.1.
Example phylogeny and expected lineage accumulation/diversification rates through time. Two clades differ in a trait/geography that results in different diversification dynamics between them. Species with tips labelled with a star share a most recent common ancestor (MRCA) that had the star trait/geography, while the sister clade with circles did not. The star clade had higher diversification rates than the circle clade, leading to the higher lineage accumulation rates and increasing diversification rates through time (solid lines) compared to the circle clade (dashed lines). Further, the star clade might have increasing diversification rates through time independent of diversity effects (i.e., diversification does not slow because of niche filling or other processes), or the diversification rate may slow towards the present, either related to diversity-dependent effects or other non-niche filling hypotheses (Moen et al. 2013).

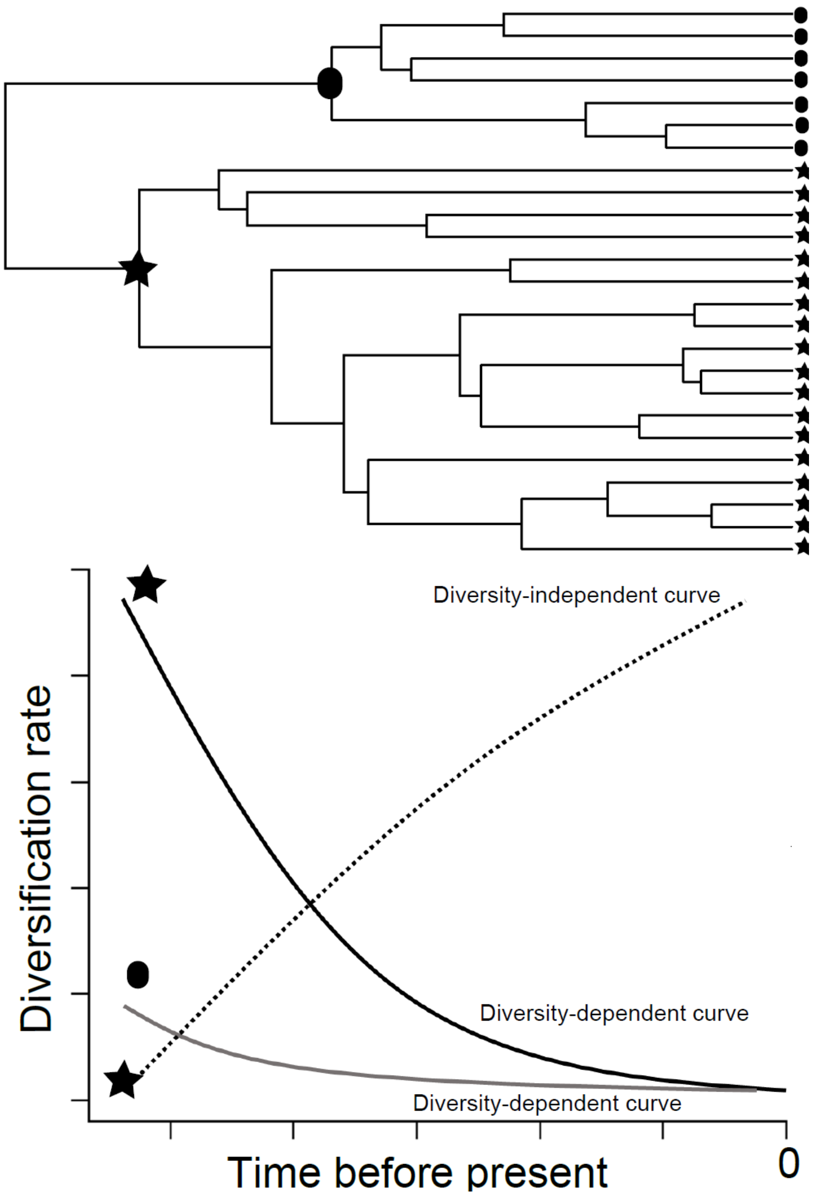

Diversity-independent curve
Diversification rate
Diversity-dependent curve
Diversity-dependent curve
Time before present
0

Figure 3.2.
Plots of the median lineage diversification and trait evolutionary rates through time (Ma) comparing the estimated rates extracted from the lemur clade and the lorisiform clade. Grey shaded areas represent the quantiles of diversification rate estimates (darker shade = 0.25-0.75, light grey = 0.05-0.95).

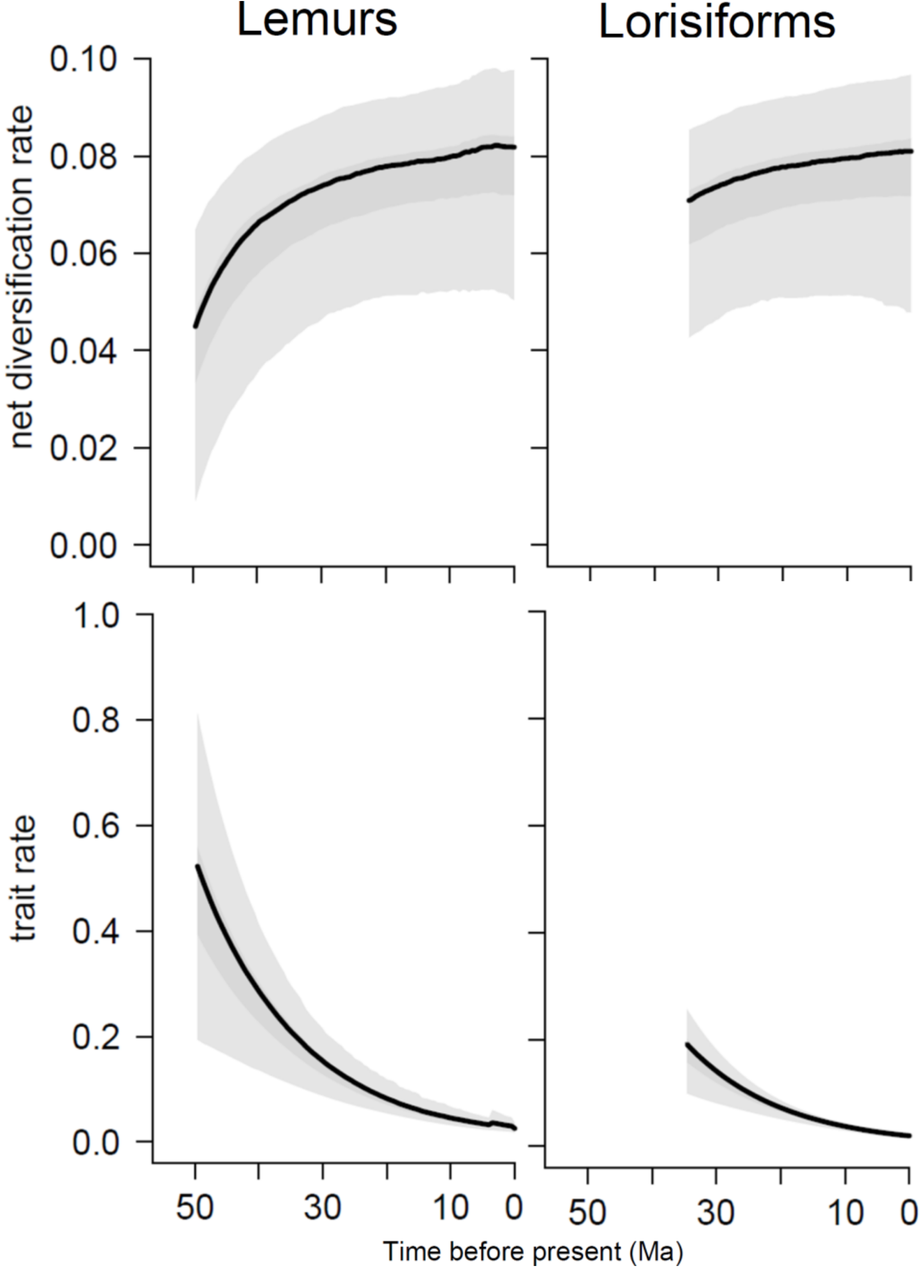


Figure 3.3.
Maximum *a posteriori* estimate of lineage and phenotypic diversification on the maximum clade credibility tree. Branch colors illustrate the mean estimate from the posterior distribution of the instantaneous rate estimate along the branches. Darker colors represent lower rates (0.01 for diversification, 0.1 for phenotype), and lighter colors higher rates (maximum values = 0.15 for diversification, 2 for phenotype). The branch leading to the lorisiforms is labelled. Crosses indicate the recently extinct subfossil lemurs.

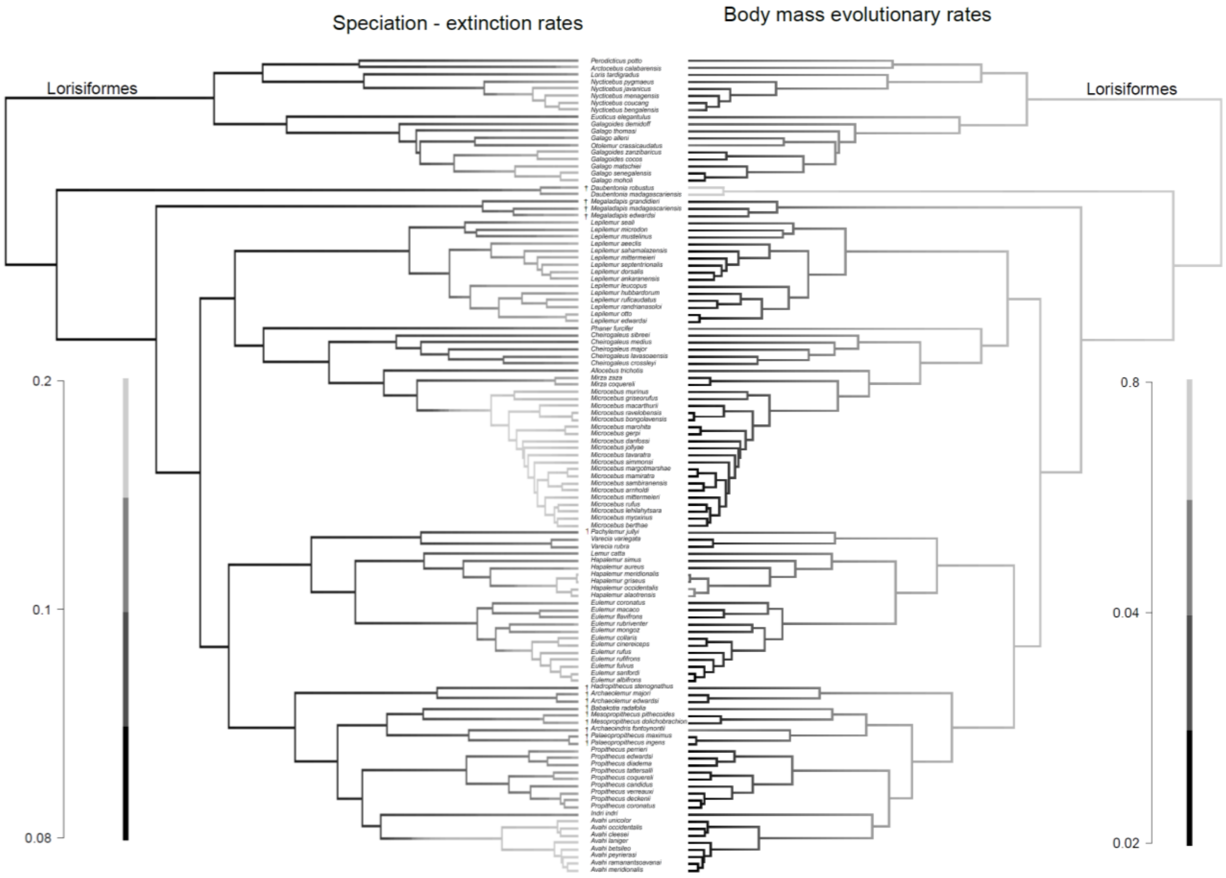
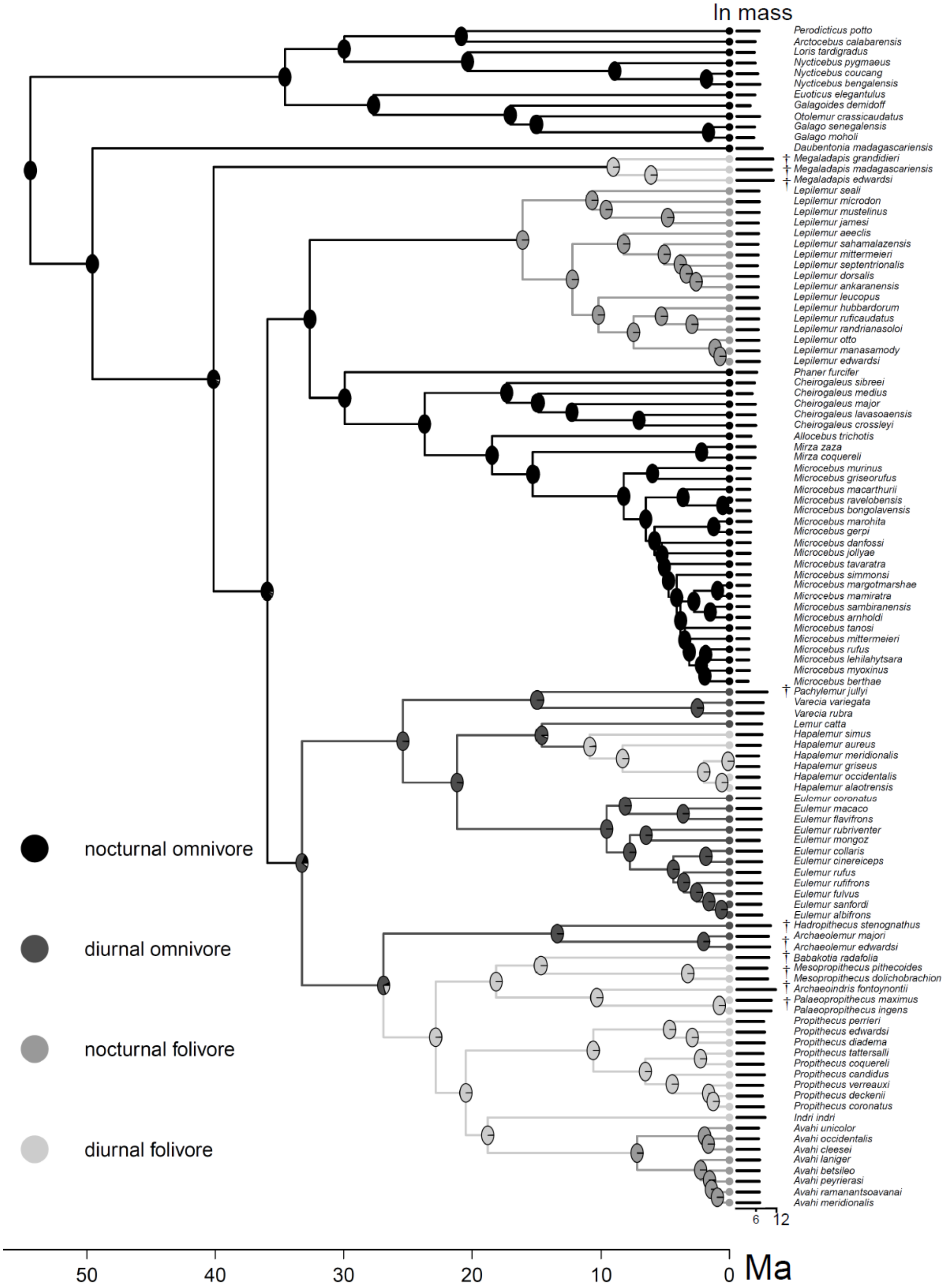


Figure 3.4.
Distribution of phenotypic and niche traits on the tree. The niche states of tips are labelled, and the scale bar next to the tips illustrates the body mass distribution (natural log transformed). Inferences of ancestral states are plotted onto nodes, with pie charts representing the proportional likelihood of the node being in each state. Crosses indicate the recently extinct subfossil lemurs.



CHAPTER FOUR

Complex biogeographic processes including dispersal and founder events explain lemur diversification on Madagascar

Abstract

The prevalence of different biogeographic processes that shape the diversity and distribution of life are still debated. Biogeographic processes, including vicariance, dispersal, extinction, and founder event speciation, are the primary modes of geographic range evolution. Madagascar is renowned for its diverse endemic biota, but the evolutionary processes responsible for that diversity are unclear. The phylogeographic patterns of several clades, especially lemurs, suggest Madagascar is subdivided geographically between the wet east and the dry west, or between the north and south. The relative roles of biogeographic processes in shaping lemur distributions on Madagascar have not been compared in an empirical framework. I used likelihood-based biogeographic models to compare the relative importance of vicariance, dispersal, sympatry, founder event speciation, and extinction. The results suggest that founder-event speciation was important to explain the distributions of species in different regions on the island; descendant species “jumped” to a new region outside the ancestral range at cladogenesis. High frequencies of dispersal and founder events were inferred between the east and west, especially through the central high plateau. The results suggest riverine dispersal barriers may have reduced dispersal between the north and south more than wet *versus* dry forest restricted species to the east or west. This is the first study on all lemurs to test which biogeographic processes have shaped the evolution of regional diversity, and the results suggest frequent dispersal, founder event speciation, and within-region speciation.

Keywords: DEC, DIVA, range inheritance, macroecology, dispersal barrier, ecological limits

Introduction

Biogeography plays a key role in speciation across scales, from local populations separated by a river to the sundering of Pangea (Avise 2000; Wiens 2012). The geographic distributions of populations affect the amount of gene flow among them, which has effects on the probability of speciation (Coyne and Orr 2004). Historical biogeography focuses on explaining patterns of species distributions through four main processes: vicariance, which is the subdivision of an ancestral range, dispersal to new ranges, sympatric speciation, and extinction (Losos and Ricklefs 2010; MacArthur and Wilson 1967; Matzke 2014; Ree and Smith 2008). Testing the relative roles of these processes in empirical systems elucidates the importance of biogeographic events (Wiens and Donoghue 2004) in the diversification of life (Crisp et al. 2011).

Differences in species richness among some clades can be explained by biogeographic processes (Wiens 2012). For example, bird species that evolved in allopatry on islands had lower diversification rates than birds that dispersed among continents (Fritz et al. 2012). One emerging concept of diversity evolution is the ecological limits hypothesis, which posits that speciation rates at continental scales are inversely related to species richness because there are ecological carrying capacities imposed by limited resources (Rabosky and Hurlbert 2015). The ecological limits hypothesis predicts that an equilibrium is reached between processes that increase regional species richness (speciation and immigration) and extinction, which decreases species richness. In contrast, evidence against equilibrium dynamics includes the prevalence of increasing species richness due to the dispersal and successful establishment of species outside their ancestral ranges. Species invasions facilitated by human-mediated dispersal as well as natural biotic exchanges consistently increase species richness and do not support an upper limit to diversity

(Harmon and Harrison 2015). For example, the diversity of frogs in Central American communities with mixed ancestry from North and South America have higher diversity than communities on either continent, suggesting that Central American communities are not saturated with species (Pinto-Sánchez et al. 2014). If biological diversity is limited by a carrying capacity, successful establishment of species via dispersal should be limited.

Madagascar is the fourth largest island in the world, and has been dubbed the eighth continent (Wit 2003). Given its biogeographic history, the diversification of life on Madagascar serves as a model of evolutionary processes. Madagascar was part of the Gondwana landmass, separated from Africa 160 million years ago (Ma), and was totally isolated after 90 Ma, when India broke away and drifted north (Samonds et al. 2012; Samonds et al. 2013; Wells 2003). The island gradually drifted from the subtropical to the tropical zone, the Indian trade winds brought warm moist air to the east coast related to increased rainfall, and unique biomes formed across the rugged terrain. Some species persisted on Madagascar from Gondwanan origins, while many others arrived by dispersal (Samonds et al. 2013; Yoder et al. 2003; Yoder and Nowak 2006). Successful colonists diversified across the myriad biomes, developing into the diverse, microendemic flora and fauna observed today.

This study addresses the biogeographic factors that shaped the diversity and distribution of species on Madagascar, and not factors that led to the origin of species on the island. Evidence from the estimated ages of extant mammal clades on the island, especially carnivores, rodents, tenrecs, and lemurs, suggests that these groups arrived via dispersal long after the island's isolation (Yoder and Nowak 2006), although some may still maintain that primates inhabited Madagascar before the break-up of Gondwana (Heads 2010; Marivaux et al. 2001). Once they arrived on Madagascar, the diversification and distribution of lemurs is a mystery. There is no

Tertiary fossil record until subfossil assemblages ~2000 years old, which reveal a diverse fauna including giant forms now extinct. Inferences of the biogeographic processes that shaped modern lemur diversity and distribution have been contentious. The competing hypotheses of evolutionary processes driving speciation differ in the relative roles of dispersal barriers, vicariance events, and ecological adaptation related to habitat suitability and niche partitioning (Vences 2009).

Biogeographic hypotheses for Madagascar megadiversity

East versus west: The biodiversity of Madagascar has been shaped by dramatic landscape changes in the deep and recent past (Samonds et al. 2013; Vences 2009; Wells 2003). The island is characterized by wet and dry tropical biomes. The east coast and eastern mountain chain receive trade winds from the Indian Ocean, and rainfall ranges from 2000-4000mm annually. West of the eastern mountains is the central high plateau, a mosaic of largely anthropogenic landscape and high montane grass and woodlands. The west coast consists of dry deciduous forest and deserts in the south. These distinct biological domains have unique suites of species, supporting the hypothesis that the diversity in Madagascar evolved due to ecological divergence (Ganzhorn et al. 1999; Godfrey et al. 1999; Kamilar 2009; Kamilar and Muldoon 2010; Martin 1995; Martin 1972; Muldoon and Goodman 2010; Richard 1991; Tattersall 1982). The modern habitats most likely originated in the Miocene, as Madagascar reached its current latitude and the trade winds from the Indian Ocean brought warm moist air to the eastern coast (Wells 2003). If the different ecoregions in eastern and western Madagascar caused geographic partitioning and speciation, then I predict cladogenesis due to range splitting of eastern and western clades, especially after the Miocene. Further, dispersal between the two regions is predicted to have been low.

North versus south: In contrast to this east *versus* west division, an alternative hypothesis suggests that rivers originating from the central high plateau were barriers to dispersal between the north and south, while they may have been corridors facilitating dispersal east and west (Ganzhorn et al. 2006; Goodman and Ganzhorn 2004a; Goodman and Ganzhorn 2004b; Martin and Martin 1990; Pastorini et al. 2003; Yoder and Heckman 2006; Yoder et al. 2005). If this hypothesis were true, then I predict a north *versus* south dichotomy, rather than an east *versus* west separation. The highlands and rivers most likely formed in the Pliocene as volcanism drove the uplift of the eastern escarpment (Wells 2003). If these rivers split formerly wide ranges and formed barriers to dispersal, then I predict higher cladogenesis due to vicariance separating northern and southern clades, especially after the Pliocene. Further, dispersal between the north and south is predicted to have been low after the Pliocene.

Pleistocene vicariance/dispersal: Geologically recent, cyclical climate change related to Pleistocene glacial events was hypothesized to cause the isolation of forest refugia around lowland watersheds. In contrast, dispersal was facilitated by rivers originating on mountains of the central highlands with stable riparian habitat (Wilmé et al. 2006). In this hypothesis, I predict cladogenesis due to vicariance in all regions starting 2.5 million years ago, and high dispersal probabilities to and from the central highlands but low dispersal among other regions at that time.

These biogeographic hypotheses have been based on different methods, including lemur phylogeography (Pastorini et al. 2003; Yoder and Heckman 2006), the fit of species distributions to proposed areas of endemism and dispersal barriers (Goodman and Ganzhorn 2004b; Pearson and Raxworthy 2009; Wilmé et al. 2006), the clustering of eastern mammal communities to the exclusion of western communities based on taxonomic compositions (Ganzhorn et al. 1999;

Kamilar 2009; Muldoon and Goodman 2010), climatic niche divergence among closely related species (Kamilar and Muldoon 2010), and habitat-suitability models (Blair et al. 2013). One approach to biogeography, event-based biogeographic inference, explicitly tests the probability of different processes and the timing of events in a likelihood framework. Then the fit of the data under the different models can be compared directly (Matzke 2014; Ree and Sanmartín 2009). In this study, I infer the most likely biogeographic history of lemur evolution by comparing the relative effects of vicariance, sympatry, founder event speciation, dispersal, extinction, and dispersal barriers.

Materials & Methods

Event-based historical biogeographic inferences optimize the likelihood of data on the species ranges and the phylogeny under different biogeographic models. The methodological workflow can be summarized as follows: 1) obtain a near-complete phylogeny for lemurs, 2) define biogeographic regions of Madagascar, 3) generate geographic range data (species presence/absence matrices) for regions, 4) optimize the evolution of geographic ranges on the phylogeny under models with different assumptions about range evolution, 5) estimate the number of biogeographic events that occurred to explain the current distribution of lemurs.

Taxa and phylogeny

I used a total evidence phylogeny that included 113 species (88%) of living and extinct lemurs (this dissertation, Chapter Two). Extant species that were missing from the original phylogeny (16 species) did not have comparable genetic loci to those used in the phylogenetic inference, but were proposed based on mitochondrial gene trees. Because comparative inferences are affected by missing data (Rangel et al. 2015), I grafted those missing species onto the phylogeny manually based on the relative position of missing species to their congeners as suggested from the original publications (Appendix III). The geographic ranges of subfossil lemur species not included here (~3 species) overlapped those that were included in the tree, and should not bias the results presented here.

Biogeographic region definitions

Defining the biogeographic regions for these analyses involved discretizing the regions. I created polygon shapefiles of biogeographic regions from available sources in a geographic information systems (GIS) database. I used three discrete region definitions (Figure 4.1). The first divided Madagascar into five bioregions simplified from the eight regions of Martin (1972): central highlands (CH), northeast (NE), southeast (SE), southwest (SW), northwest (NW). I created polygon shapefiles of the five simplified bioregions by georeferencing the map in Pastorini et al. (2003) in QGIS (Quantum GIS Development Team 2015), with eight georeference points used to maximize the fit of the map to the GIS. The second and third regional definitions were based on the hypotheses that the major divisions in Madagascar are east *versus* west or north *versus* south. The east / west regions divided Madagascar at approximately 47° E, roughly following the division of wet forests to the east and dry forest to the west. The north / south regions divided Madagascar at approximately 20°S, corresponding to the Tsiribihina river to the west and the Mangoro river to the east, each with their headwaters near the Ankaratra massif in central Madagascar. These three biogeographic region definitions summarize some of the inferred major biogeographic areas of endemism hypothesized for Madagascar (Ganzhorn et al. 2006; Vences 2009; Yoder and Heckman 2006), but cannot explicitly test hypotheses that have involved more regions (>20 regions Wilmé et al. 2006). Increasing the number of regions in the analysis increases the total number of possible range combinations and quickly becomes intractable, especially with trees similar to the size in this study (Matzke 2014).

Lemur geographic range data

To create presence/absence matrices of lemur distributions in the defined biogeographic areas, I obtained polygon shapefiles of extant lemur range maps from the IUCN terrestrial mammal database (http://www.iucnredlist.org/technical-documents/spatial-data, accessed 2/18/2015). I verified each lemur range against original and secondary sources to verify the limits of species distributions (Mittermeier et al. 2010; Muldoon and Goodman 2010), editing polygons where necessary. These lemur distribution polygons were included with the biogeographic region polygons in the GIS, and species presence/absence matrices for each region were tabulated using the *intersect* function in the R package *raster* (Hijmans 2015; R Core Team 2014). Presence/absence matrices were then verified against literature sources and reports of ground-truthed surveys (Mittermeier et al. 2010; Muldoon and Goodman 2010; Schwitzer et al. 2013). Extinct lemurs lacked range maps and rather than attempt to create them based on the data available, I manually coded their regional presence/absence based on the literature (Godfrey et al. 2010). I included *Indri* and *Hapalemur simus* as present in the NW region because, although they are now absent from the region, their remains have been found in subfossil assemblages in that region (Ankarana, Anjohibe) and those populations have since gone extinct (Jungers et al. 1995). The regional presence/absence matrices, region maps, and GIS files are available in the supplemental information and have been deposited in the Dryad archive.

Event-based historical biogeography models

I inferred lemur ancestral range evolution using parametric event-based biogeography models, as implemented in the R package BioGeoBEARS (Matzke 2014). In this framework, dispersal is inferred when descendants add a new range to the ranges of the ancestors, and it is assumed to occur along branches (anagenetic). At branching points on the tree (cladogenesis events), widespread ancestral ranges can be split by descendants (vicariance), descendants can inherit the exact ancestral range or a subset of it (sympatry), or descendant lineage can be in an entirely new area not shared with the common ancestors (founder-event speciation, Table 4.1, after Matzke 2014). Each kind of biogeographic event is a parameter in the models and has a weight for the per-event probability in a joint model explaining the evolution of ranges. In this way, models can be set to compare the importance of each parameter, or parameter weights can be estimated. For example, a vicariance-only model would set the dispersal and founder event speciation parameters to zero, while a model favoring dispersal would set vicariance to zero. The likelihood of the data under these two models can then be compared, allowing inferences of which modes of biogeographic evolution explain the data better. Species and ancestors can be coded and inferred to have widespread distributions, which is especially advantageous in this system where many species are found in more than one biogeographic region. Inferences of ancestral ranges are expressed as the proportional likelihood of node state estimates, explicitly quantifying the uncertainty in ancestral range inference.

Model comparison

In BioGeoBEARS, published biogeographic models can be replicated by fixing the per-event probability of each kind of event according to the assumptions of the original models, or estimating them as free parameters so that the user can assess their relative impact on biogeographic inferences. I compared the fit of the biogeographic data under the following four biogeographic models, three that mimic or replicate previously published models and one that consists of a mix of the assumptions in published models, as well as those same models with the addition of the founder event parameter.

1) A maximum likelihood approximation of the dispersal-vicariance model (DIVA, Ronquist 1997) allows dispersal, extinction and wide vicariance in which a widespread ancestor has descendants which inherit a subset of one or more of the ancestral ranges, but does not allow subset or widespread sympatry.
2) The dispersal-extinction-cladogenesis model (DEC, Ree and Smith 2008) is exactly replicated in BioGeoBEARS by allowing subset- but not widespread sympatry, and only allowing narrow vicariance (daughter species of vicariance events inherits a single range from a widespread ancestor).
3) A model allowing exact range inheritance sympatry as the only cladogenetic event approximates the BAYAREA algorithm (Landis et al. 2013) and is also similar to estimating ancestral character states using a discrete-character Markov model (Matzke 2014).
4) A variant of the DEC model in which both narrow and widespread sympatry and vicariance were allowed (DEC-like).

Dispersal probability transition matrix

The likelihood-based parametric biogeographic analysis used here also allows the user to specify hypothesized probabilities of dispersals among regions as a transition matrix and explicitly test the likelihood of certain transitions. Without a user-specified matrix, dispersal probabilities among regions is assumed to be 1. In the five-region definition, I compared the fit of each of the four biogeographic models described above with and without a dispersal multiplier transition matrix based on region adjacency that did not change through time. Nonadjacent regions, those that did not directly share a border, had 0 dispersal probabilities, reflecting the hypothesis that it was impossible for a lineage to spread to a nonadjacent region without first passing through an adjacent one. Adjacent regions were those that shared borders (NE+NW, NE+SE, NW+SW and each region + CH) and had dispersal probability of 1, except for SE and SW which share a small border separated by the Anosy mountain chain (probability = 0.5). This adjacency matrix is similar to one used in a similar study of Malagasy faunal biogeography (Miraldo and Hanski 2014b). In the east / west and north / south region definitions, I compared models with asymmetrical transition matrices in which probability of dispersing from N or E to S or W = 0.5, while the reverse = 0.25, as well as the inverse of these matrices (Appendix III).

The dispersal multiplier transition matrices can be time-stratified to test hypotheses of changes in dispersal probability through time. To test the ecoregion / river barrier hypothesis (after Martin 1972) and Pleistocene watershed refugia / highlands dispersal hypothesis (Wilmé et al. 2006), which make temporally explicit predictions about changes in dispersal probability, I compared the best fitting biogeographic model with the following two time-stratified dispersal probability transition matrices. (1) Dispersal probability was based on adjacency until the Miocene, when the divisions among wet, dry, and spiny desert habitats most likely had their current distribution (Wells 2003), and dispersal among habitat types was low (0.001). In the Pliocene, when most modern rivers were forming their current courses, dispersal among regions separated by rivers was low (0.001). (2) Pleistocene watershed refugia, highlands dispersal hypothesis (Wilmé et al. 2006): Dispersal probability was based on geographic distance until the Pleistocene, when dispersal among watershed regions was low and dispersal to/from central highlands was high (Appendix III).

Because these models are implemented in a common likelihood-based framework, model comparison is possible by using likelihood ratio tests for nested models and information theoretic criteria for non-nested models. I assessed model fit with the Akaike information criterion penalized for small sample size (AICc). I compared each model with and without the addition of a founder-event parameter and with/without addition of dispersal probability transition matrices. The model with the best fit had to lowest AICc, AIC weight > 0.9, and an AIC > 3 points lower than the next best model (Burnham and Anderson 2002).

Quantifying the number of events: Estimating the actual number of biogeographic events that are inferred to occur on the tree is done using Bayesian stochastic mapping (BSM). Given the data (presence/absence in different ranges, phylogenetic tree) and the biogeographic model, the evolution of ranges is simulated and the number of events across simulations is tallied (Matzke unpublished). The BSM procedure was used to quantify the number of each kind of biogeographic event (vicariance, founder event, dispersal, sympatry, extinctions) for the best model with each area definition.

Results

Model comparison

Five area definition: The best-fitting model of historical biogeography, with 70% of the model weight, was Model 4 – DEC-like, which included a combination of narrow and wide vicariance, subset, narrow, and wide sympatry, dispersal, extinction, with the founder event parameter and the adjacency-based dispersal probability transition matrix (Table 4.2). According to this model, lemur distributions are explained by a combination of cladogenetic and anagenetic range evolution events and no change in dispersal probabilities through time. The next best model, with 27% of model weight, was the same DEC-like model with the founder event parameter, but included the time-stratified dispersal matrix based on the Pleistocene watershed refugia / highlands dispersal hypothesis (Wilmé et al. 2006). The same model with the time-stratified dispersal transition matrix based on the Miocene habitat barrier and Pliocene river barrier hypothesis had low model support (<0.1% model weight, Table 4.2).

East versus west definition: The DEC model with founder event speciation fit the east / west dataset better than other models, and asymmetrical dispersal probabilities fit the data marginally better than equal probabilities but those two models had comparable support (Table 4.3).

North versus south definition: The DEC model with founder event speciation fit the north / south dataset best, and adding an asymmetrical transition probability model in which dispersal from south to north was higher than *vice versa* improved model fit (Table 4.4).

Ancestral area estimation

Five area definition: The inferences of ancestral ranges were equivocal for deep nodes, but there were high probabilities (>50% proportional likelihood) of particular ancestral areas for some genera and lineages within genera (Figure 4.2). For some genera, node state estimates were widespread, for example, including a combination of CH and SW for *Megaladapis, Hadropithecus,* and *Palaeopropithecus,* or CH, NE, NW, and SE for *Hapalemur* and *Cheirogaleus.* Widespread ranges were subdivided by descendants via vicariance and subset sympatry events. Examples of subset sympatry include some lineages within the genera *Propithecus* and *Avahi,* in which one daughter species inherits a widespread ancestral range, while the other daughter buds off in a subset of the widespread ancestral range (Figure 4.2). Several nodes, especially lineages within genera (e.g., *Lepilemur, Eulemur, Microcebus*), had strong support for the NW region as the ancestral range, with daughter species retaining that range, suggesting within-region sympatric speciation. Founder-events were inferred from species that occupied regions not shared with the ancestor. Examples of founder events include within the genus *Microcebus*, in which many of the nodes were inferred with strong support to occur in the NE, while descendants occurred in other regions (e.g., NW, SE, and SW). Ancestral range estimates for the extinct lemurs suggested widespread ancestors with distributions including the SW, NW, and CH, while extant species were rarely inferred to have ancestral ranges in the SW.

East versus west definition: The eastern region was most frequently inferred as the ancestral region in the east / west biogeographic definition (Appendix III Figure 1). Deep nodes were inferred to have ranges in the east with >50% proportional likelihood, and nodes of most genera were inferred to have ranges in the east with 50 – 100% proportional likelihood. Exceptions include the genus *Lepilemur*, which had >50% proportional likelihood of being widespread (east *and* west), and two lineages within the genus split into eastern and western clades by vicariance. The genera *Propithecus* and *Avahi* had ~50% support for widespread ancestors subdivided into eastern and western clades via vicariance, but the results for these clades are less strongly supported than *Lepilemur*. *Eulemur* most likely had its origins in the west, a region it colonized via dispersal from an eastern ancestor.

North versus south definition: The ancestral state estimates for the north / south biogeographic definition were more equivocal than for east *versus* west, especially for deep nodes (Appendix III Figure 2). The proportional likelihoods strongly supported a northern origin for some clades, especially the clade with the extinct giant sloth lemurs and the living *Propithecus, Indri* and *Avahi*.

Stochastic mapping of events

Five area definition: Bayesian stochastic mapping was used to simulate 200 range evolution histories on the phylogeny given the best biogeographic model, and estimates of the number of range-shift events were obtained. A mean total of 181.8 range-shift events were recorded (+/- standard deviation of 4.57 events), most of which were anagenetic dispersal events (39% of events), adding ranges to the lineage distribution without speciation (Table 4.5). The results suggest that speciation within regions was relatively high, as inferred from the number of sympatric speciation events (39%). At the level of resolution for these five areas, this result may indicate further geographic partitioning within regions that may have resulted in allopatric speciation. Founder events explain more geographic range shifts (14%) than vicariance (9%), but again this may be due to the coarse definition of areas that may not capture within region vicariance events.

Tabulating the inferred number of events via stochastic mapping, specific dispersal and founder event “jumps” among regions were enumerated (Figure 4.3). Anagenetic dispersal was high to and from the central highlands from other regions, intermediate between NW and NE, and low between SW and SE. Dispersal was higher from northern to southern regions than *vice versa* (Figure 4.3a). Cladogenetic dispersal, i.e., founder events, occurred most frequently between NE and NW, as well as from NE to SE (Figure 4.3b).

East versus west definition: Regional sympatry was the highest cladogenetic event (56% of 135 events) and vicariance was low (4% of events), as would be expected given the coarse definition of regions (Appendix III Table 1). Founder events (11%) and dispersal (17%) were relatively high, and most of the range shifts were from east to west (mean dispersal east to west = 16.48 +/- 2.76, dispersal west to east = 6.83 +/- 2.63; mean founder events east to west = 10.14 +/- 2.61, west to east = 5.35 +/- 2.59).

North versus south definition: As with the east / west definition, sympatry was high in the north / south regions (53% of 135 events) and vicariance was low (4%, Appendix III Table 2). Founder events (15% of events) were more frequent from north to south (mean=11.16 +/-2.49) than *vice versa* (mean=9.29 +/- 2.75), while anagenetic dispersal was higher from south to north (mean =

13.5 +/- 3.13) than *vice versa* (mean = 9.96 +/- 3.07). These results suggest that dispersal from north to south resulted in speciation, while dispersal from south to north did not.

Vicariance events were less frequent than regional sympatric speciation events with all three area definitions, but this is most likely an artifact of the low geographic resolution of the regions. Many species that are sympatric within a region have allopatric distributions at finer scales, and within-region sympatric speciation may actually reflect vicariance at higher resolution. The trade-off between regional sympatric speciation and vicariance with geographic resolution is clearly illustrated by the higher ratio of sympatric to vicariant events in the two-area definitions than the five area definition. This result emphasizes that area definitions are important for interpreting inferences of biogeographic events.

Discussion

In this study, I found support for multiple biogeographic processes shaping the range evolution and species richness of lemurs. Vicariance, dispersal, regional sympatric speciation, and founder event speciation all played roles in lemur diversification. Temporal changes in dispersal probability related to the emergence of biogeographic barriers did not explain the data better than dispersal probabilities based on adjacency. The central highlands played a key role as a dispersal corridor and patterns of higher dispersal from east to west than *vice versa* were observed. Dispersal and founder events between the northeast and northwest regions were common, as well as from north to south. The results strongly support a hypothesis of lemur evolution that involves east / west connectivity via the central highlands.

Evidence for biogeographic hypotheses

The biogeographic causes of species distributions in Madagascar, especially areas of high microendemism, have been the subject of great debate. The gradients in rainfall from east to west create distinct biological domains, and patterns of some lemur species' distributions correspond to different domains (Blair et al. 2013; Martin 1972; Pastorini et al. 2003). Within domains, several key rivers have also been hypothesized to act as barriers to dispersal (Martin 1972; Pastorini et al. 2003). These observations led to hypotheses of biogeographic evolution via ecological adaptation to eastern wet and western dry forests, and the central highlands as a dispersal barrier. On the other hand, phylogeographic patterns of mouse lemurs, *Microcebus*, indicated that species formed monophyletic northern and southern clades, suggesting a north / south dispersal barrier rather than an east / west division (Ganzhorn et al. 2006; Yoder and Heckman 2006). East / west connectivity may have been facilitated by riverine forests that spanned the central highlands, while north / south dispersal may have been limited by river barriers with high elevation headwaters (Goodman and Ganzhorn 2004a; Goodman and Ganzhorn 2004b). Considering Pleistocene climate change, during dry glacial periods, forests in lowlands were hypothesized to have contracted and fragmented, while mountains with stable rivers maintained forest habitat and acted as dispersal corridors (Wilmé et al. 2006). These competing hypotheses have never been compared using event-based parametric biogeography techniques until now, and the results shed light on the competing modes of speciation.

I found that dispersal to and from the central highlands and between the northeast and northwest was common. Dispersals were more likely from east to west, and fewer occurred between the northern and southern regions than between the northeast and northwest. The model with the strongest support had dispersal probabilities based on the adjacency of regions, and temporal changes in dispersal probabilities did not explain the data better than static probabilities. Founder event speciation was important; there were as many as 25 instances of a lineage dispersing to an area outside of the ancestral range at speciation, mostly between the northeast and northwest. The results therefore provide better support for the north / south dispersal limitation than the east / west delineation, and the central highlands may have facilitated dispersal among regions.

Debate surrounds the role of the central highlands in Madagascar biogeography. The highlands now consist predominantly of mixed anthropogenic landscape, with pastures, agricultural fields, abandoned grasslands, exotic tree plantations, and human settlements. Despite the denuded current state of the central highlands, its paleoecology and remaining forest patches 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 now found at the highest elevations, but there was a distinct shift to woodland/savannah mosaic during warm, moist conditions after the last glacial maximum (Burney et al. 2004). The subfossil lemur site Ampasambazimba is located in the central western highlands and the paleoecology indicates it was a wooded marsh with ~20 sympatric, forest-dwelling lemur species, hippos, and other humid forest elements (Godfrey and Jungers 2003). Ambohitantely, Kalambatritra, and Zombitse are examples of modern highland forest fragments with both wet and dry forest characteristics. These fragments may be relicts of a pre-human mosaic highlands landscape (Ganzhorn et al. 2006). The mounting evidence for past connectivity between the east and west refutes the long-standing hypothesis that the eastern and western biotas were ecologically and evolutionarily divergent.

Biogeographic events in deep time may reflect responses of organisms to climate change. The Pleistocene watershed refugia / highlands dispersal hypothesis explicitly predicted changes in dispersal probability in the Pleistocene. The timing of the formation of habitats, rivers, and mountains is only vaguely estimated for Madagascar, which has no paleoecological record earlier than the Pleistocene (Burney et al. 2004). But considering climate change globally may lend some insights into causes of range shifts in lemurs. The Eocene-Oligocene boundary (~33.9 Ma) is a time of marked global cooling and drying related to the formation of Antarctic glaciers (Coxall et al. 2005). Madagascar was also farther south by 4-7°, which may have been related to cooler climates than today (Wells 2003). At the same time, major extinction events and faunal turnover in primate communities occurred in North America and Afro-Arabia (Seiffert 2007). The ancestral range estimates for Eocene nodes in the lemur tree were largely equivocal, and extinctions may have erased a signal of historical biogeography (Losos and Glor 2003). There was support for ancestral ranges in the NW and CH throughout most of the Oligocene and into the Miocene. During the late Miocene and Pliocene, ranges expanded in many clades, and increasing range shifts towards the present may be related to the increasing speciation rates observed in an analysis of lemur diversification dynamics (this dissertation, Chapter Three). The temporally explicit biogeographic hypotheses tested in this study give great insights into the mechanisms of lemur diversification, and similar analyses with other clades illustrate the complexity of biogeographic processes.

Models of biogeographic evolution in Malagasy herpetofauna have also suggested that no single mode of geographic range evolution can account for all the variation in species distributions (Brown et al. 2014; Vences 2009). While there was general concordance between reptiles and amphibians in peaks of species richness in the north and east of Madagascar, some reptile groups had their areas of endemism in the southwest (Brown et al. 2014). Malagasy dung beetles exhibited a complex biogeographic history with all clades showing strong evidence for origins in northern Madagascar, followed by the expansion and subsequent allopatric diversification of species that evolved large body size (Miraldo and Hanski 2014). Within lemur genera, some lineages were found to diverge between eastern and western clades due to vicariance (e.g., *Lepilemur*), while other lineages diverged via dispersals from north to south (e.g., *Microcebus*). The frequency of dispersal events strongly suggested that east / west connectivity facilitated movement among regions, especially through the central highlands. This study is the first to empirically test the support for competing biogeographic hypotheses and quantify the evolutionary mechanisms responsible for lemur diversification and distribution. The results compliment recent findings from other clades that illustrate simple biogeographic models cannot explain the distribution of complex organisms.

Implications for ecological limits hypotheses

The ecological limits hypothesis predicts that the species richness of ecological communities is limited by a resource-related carrying capacity leading to equilibrium diversification dynamics (Rabosky and Hurlbert 2015). If the capacity for a region to support species is limited by diversity-dependence, then within-region speciation should decrease, dispersal into the region from outside should be low, and/or increasing species richness via speciation and dispersal should be balanced by extinction. I found that lemur speciation rates increased through time, rather than decline with increasing species diversity (this dissertation, Chapter Three). These findings seemed to refute the ecological limits hypothesis, and led me to ask what caused increasing speciation rates through time? Insights from the biogeographic inferences presented here may explain the increasing speciation rate observed for lemurs as well as shed light on the debate over ecological limits.

The biogeographic inferences for lemur range evolution suggested that most regions, especially the NW, had high within-region diversification, and regions were also repeatedly colonized by dispersal, including founder event speciation. The prevalence of these two processes which both increase species richness refutes equilibrium dynamics because regional species diversity should plateau and rates of species accumulation should decrease as species richness increases. Further, if rates of immigration declined due to regional species saturation, then a model that included decreasing dispersal probability in the recent past should have had a better fit to the data than a static dispersal probability. Counter to this prediction, decreasing dispersal probabilities did not explain the data better than dispersal probability based on adjacency. The regions of Madagascar had properties consistent with open communities susceptible to invasion, rather than closed systems that are maximally full of species (Harmon and Harrison 2015). Proponents of the ecological limits hypothesis explain that equilibria shift through time rather than remain static (Rabosky and Hurlbert 2015). Rather than assume species diversity oscillates around some multi-species carrying capacities which vary by geographic and temporal scale, however, it may be more accurate to hypothesize that evolution is not limited by carrying capacities. Instead, diversification rates are related to lineage-specific differences in vagility and propensity for speciation, which in turn are related to species traits, geologic history, and global climate change in deep time. The biogeographic events inferred and reported here may have promoted increasing speciation rates in lemurs and should be explored in other taxa to understand patterns of diversification through time in Madagascar and globally.

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Tables and figures

Table 4.1.
Definitions of the kinds of biogeographic events that are parameterized in the biogeographic analyses. Definitions follow those of Ree and Smith (2006), Ronquist (1997) and Matzke (2014). Examples are given for a simple four-area system: A, B, C, and D. The second column specifies whether the event is cladogenetic, occurring at branching points on the phylogeny, or anagenetic, occurring along the branches.

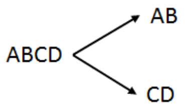
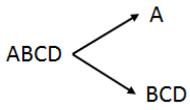
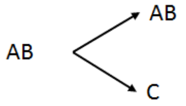
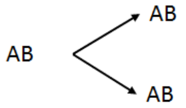
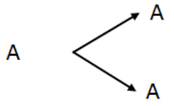
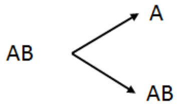
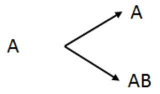
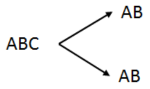
Biogeographic event	**Cladogenetic or anagenetic**	**Definition**	**Example**
Vicariance	Cladogenetic	The ancestral range is inferred to include more than one area, and descendants inherit non-overlapping parts of that range. Vicariance can be subdivided into wide and narrow kinds. In wide vicariance, daughter species may inherit more than one area of the ancestral range. In narrow vicariance, daughter species may inherit only one area from the ancestral range.	Wide vicariance:  Narrow vicariance: 
Founder event	Cladogenetic	One daughter species occurs in an area outside the range of the ancestor	
Exact-range inheritance sympatry	Cladogenetic	Both daughter species occur in the same overlapping range as the ancestor. In this definition, sympatry is defined broadly as occurring within the same region, which is not to say that species actually speciated in the same local communities. Exact-range sympatry inheritance sympatry can be either wide (including more than one area) or narrow (one area).	Wide:  Narrow: 
Subset sympatry	Cladogenetic	One daughter species occurs in one area inherited from a widespread ancestor, while the other daughter occurs in more than one area, and daughter ranges overlap.	
Dispersal	Anagenetic	Daughter species inherits ancestral range as well as an additional area not shared with the ancestor.	
Extinction	Anagenetic	Daughter species does not occur in one of the ancestral areas.	

Table 4.2.
Comparison of biogeographic models of lemur range evolution ranked by model support. The parameters included in each model, model code name, dispersal, extinction and founder event per-event probability weights, and model fit statistics are given (k = # of parameters, LnL = log likelihood). The best model included wide and narrow vicariance, subset sympatry, exact range inheritance sympatry, founder event speciation and adjacency-based dispersal multipliers. The next best model had the same cladogenesis model but with changes in dispersal probabilities corresponding Pleistocene watershed hypothesis. Dispersal, extinction and founder parameters values represent the weights applied to the likelihood that each parameter caused a change in geographic state on the tree, averaged across all changes.

Model specifications	Dispersal	Extinction	Founder	LnL	K	AICc	Delta AICc	AIC weight
Vicariance*, sympatry, subset, founder, dispersal, extinction + adjacency *wide and narrow (DEC-like + J)	**0.02**	**<0.001**	**0.1**	**-288**	**7**	**594.79**	**0**	**0.72**
Pleistocene refugia/retreat-dispersal watersheds (DECJ + time-stratified dispersal probabilities)	0.03	<0.001	0.12	-290	7	596.68	1.89	0.28
Vicariance, subset, sympatry, founder, dispersal, extinction + adjacency (DECJ)	0.03	<0.001	0.1	-300	3	605.5	10.7	0.003
Vicariance*, sympatry, equal prob, founder, extinction + adjacency *wide vicariance (DIVA-like + J)	0.03	<0.001	0.09	-307	3	621.02	26.22	0
Habitat + river barrier hypothesis (DECLIKEJ + time-stratified dispersal probabilities)	0.08	0.007	0.12	-306	7	627.93	33.14	0
Vicariance, subset, sympatry, dispersal, extinction + adjacency (DEC)	0.03	<0.001	0	-312	2	628.59	33.8	0
Sympatry, founder effect, dispersal, extinction + adjacency (BAYAREA-like + J)	0.02	<0.01	0.17	-316	3	637.29	42.49	0
Vicariance*, sympatry, dispersal, extinction *wide (DIVA-like)	0.04	<0.001	0	-323	2	650.33	55.54	0
Vicariance*, subset, sympatry, dispersal, extinction *narrow (DEC)	0.02	<0.001	0	-324	2	651.21	56.42	0

Sympatry, dispersal, extinction+ adjacency (BAYAREA-like)	0.03	0.09	0	-358	2	719.59	124.8	0

Table 4.3.

Biogeographic models ranked by model fit for the east *versus* west biogeographic definition. As for Table 2, model codes, per-event weights of the probability of dispersal, extinction and founder events, as well as model fit statistics are given. The two models that fit the data best were the DEC + J models with and without an asymmetrical transition matrix. The DEC model allows narrow vicariance, subset- wide- and narrow- sympatry, dispersal, extinction and founder event speciation. The transition matrix 2 had higher dispersal probability from east to west (0.5) than the reverse (0.25), while transition matrix 1 had the opposite asymmetrical transition matrix. See the text for details on DIVA and BAYAREA biogeographic event assumptions.

Model	**dispersal**	**extinction**	**J**	**LnL**	**K**	**AICc**	**delta AICc**	**AIC weight**
DEC+J transition matrix 2	0.08	<0.001	0.28	-98.91	3	203.8	0	0.59
DEC+J	0.03	<0.001	0.1	-99.41	3	204.8	1	0.36
DEC+J transition matrix 1	0.08	<0.001	0.21	-101.3	3	208.6	4.8	<0.01
DEC	0.04	<0.001	0	-105.4	2	214.9	11.1	<0.01
DIVA-like+J	0.04	0.001	0.08	-106.7	3	219.4	15.6	<0.01
BAYAREA-like+J	0.02	<0.001	0.13	-108.2	3	222.4	18.6	<0.01
DIVA-like	0.06	0.001	0	-115.1	2	234.2	30.4	<0.01
BAYAREA-like	0.04	0.03	0	-147.1	2	298.2	94.4	<0.01

Table 4.4.
Biogeographic models ranked in order of model fit for the north *versus* south biogeographic definition. The best fitting model was DEC + J with an asymmetrical transition matrix in which the probability of dispersal from south to north was higher (0.5) than the reverse (0.25). Transition matrix 1 had the reverse asymmetry.

Model	**dispersal**	**extinction**	**J**	**LnL**	**K**	**AICc**	**delta AICc**	**AIC weight**
DEC+J transition matrix 2	0.09	<0.004	0.4	-93.57	3	193.14	0	0.92
DEC+J	0.03	<0.002	0.12	-96.1	3	198.19	5.05	0.07
DEC+J transition matrix 1	0.07	<0.003	0.2	-99.5	3	205.05	11.91	<0.001
DIVA-like+J	0.05	<0.006	0.09	-103.05	3	212.11	18.97	<0.001
BAYAREA-like+J	0.02	0.002	0.11	-104.79	3	212.58	19.44	<0.001
DEC	0.05	<0.001	0	-111.41	2	226.83	33.69	<0.001
DIVA-like	0.06	<0.005	0	-111.76	2	227.52	34.38	<0.001
BAYAREA-like	0.06	0.04	0	-158.75	2	321.5	128.36	<0.001

Table 4.5.
Summary of the number and proportion of biogeographic events simulated on the phylogeny under the best biogeographic model with the five area bioregion definition using Bayesian stochastic mapping. Founder = founder event speciation, dispers = anagenetic dispseral, ext = extinction, subset = subset sympatry, vicar = vicariance, symp = exact-range inheritance sympatry.

	founder	%	dispers	%	ext	subset	%	vicar	%	symp	%	Total events
means	25.09	13.80	70.53	38.80	0.00	22.91	12.60	16.79	9.24	46.51	25.58	181.80
stdevs	4.38		4.33		0.00	4.49		3.83		3.79		4.57

Figure 4.1.
Maps of Madagascar with the three area definitions. A) The five ecoregions simplified from the eight regions of Martin (1995), B) the east *versus* west division, C) the north *versus* south division.

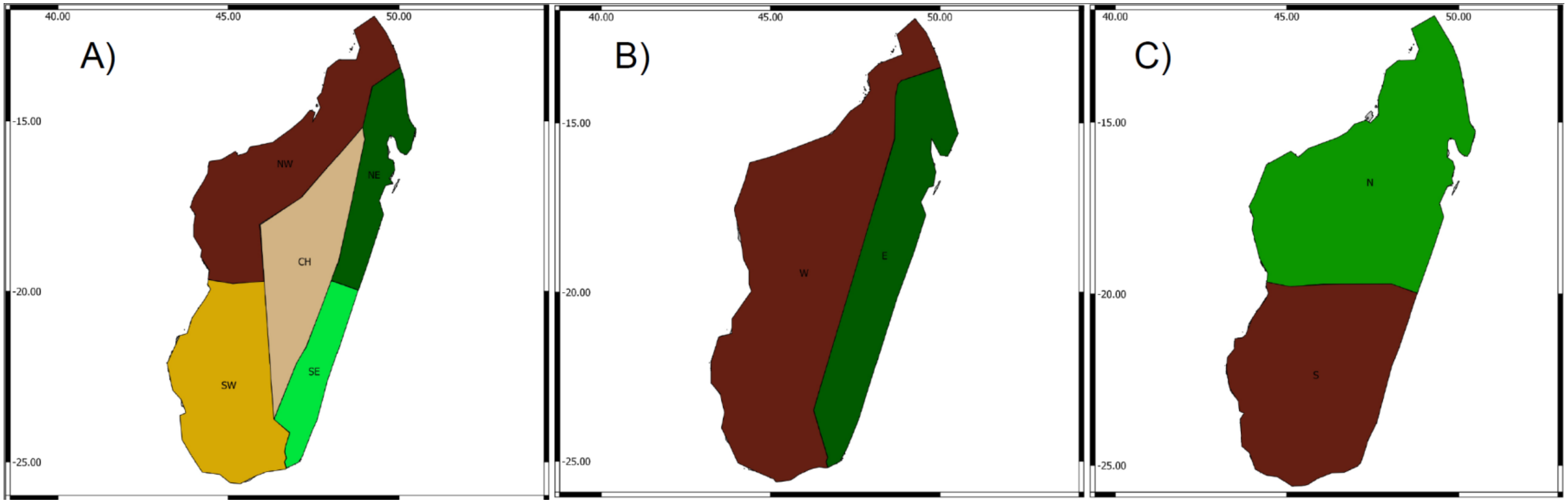


Figure 4.2.
Ancestral range inferences from the best-fitting model of historical biogeography, from BioGeoBEARS (Matzke 2014). The best fitting model included estimates of vicariance, with descendant ranges of various sizes, subset sympatry, exact range inheritance sympatry, founder event speciation and dispersal multipliers based on the adjacency of regions. Color codes correspond to range states as depicted in the legend. The pie charts at nodes represent the proportional likelihood that the ancestral ranges were in each state. Widespread (blue) indicates occurrence in more than one region, and equivocal indicates that the proportional probabilities were equally low across a number of possible range states. Region abbreviations are as follows: CH = central highlands, NE = north east, NW = north west, SE = south east, SW = south west.

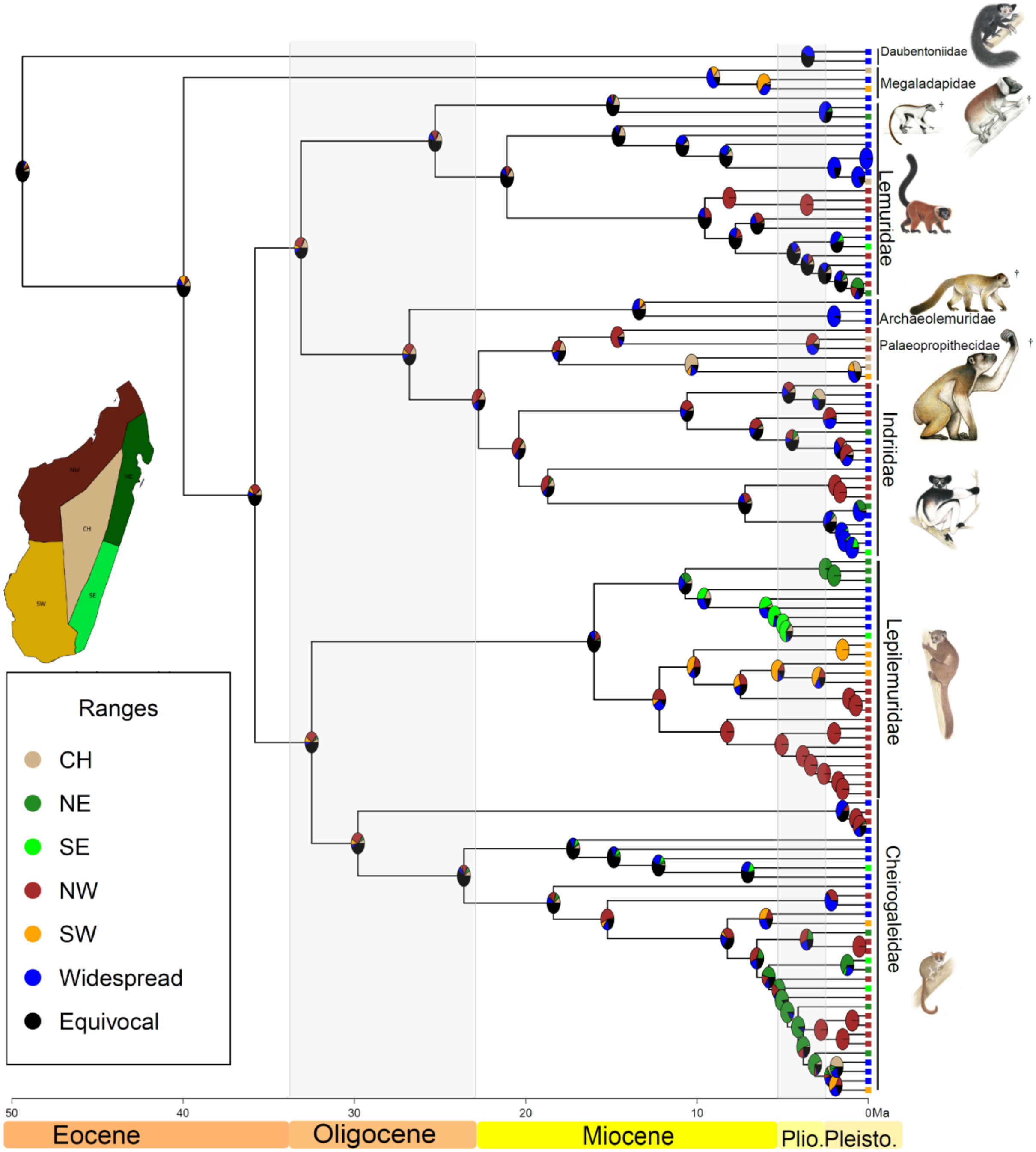
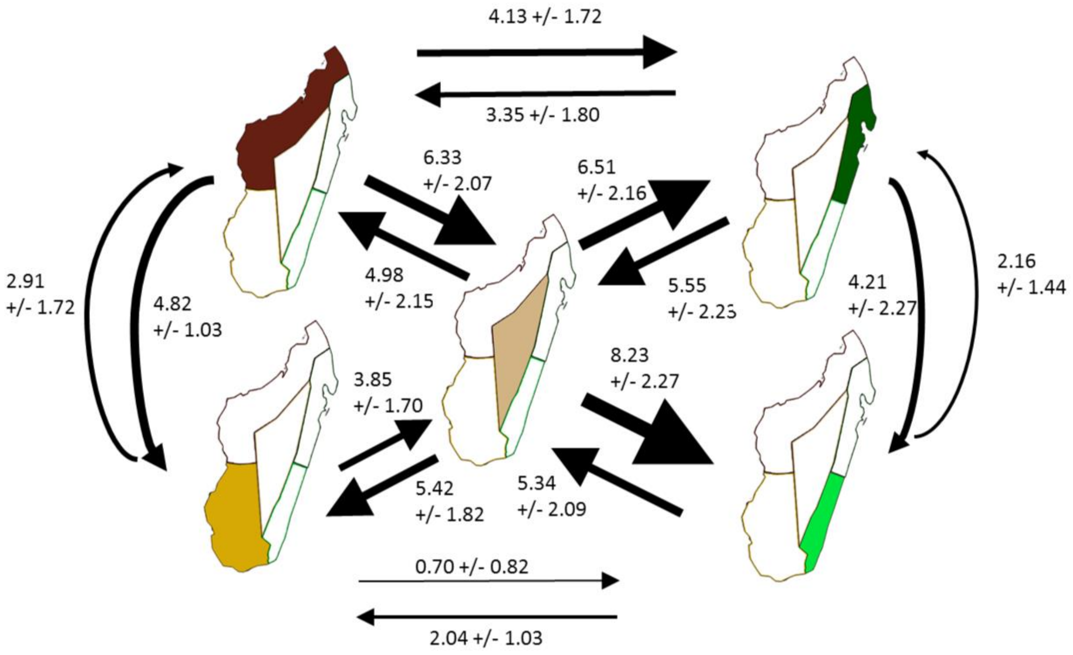

Daubentoniidae
Megaladapidae
Lemuridae
Archaeolemuridae
Palaeopropithecidae
Indriidae
Lepilemuridae
Cheirogaleidae
NW
NE
CH
SW
SE
Ranges
CH
NE
SE
NW
SW
Widespread
Equivocal
50
40
30
20
10
0Ma
Eocene
Oligocene
Miocene
Plio.Pleisto.

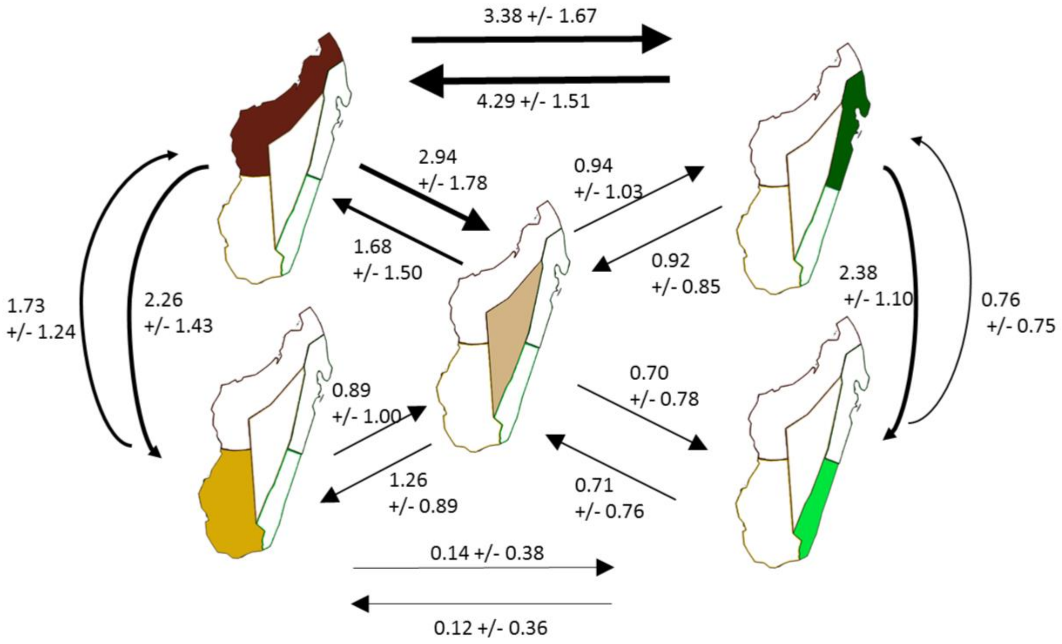
Figure 4.3.

Inferred number of dispersal and founder events explaining the movement of lemur lineages among regions. The numbers are the mean +/- standard deviation number of events from 200 simulated geographic histories under the best fitting biogeographic model using Bayesian stochastic mapping. The arrows indicate the direction of movement and the width is proportional to the mean number of inferred events. A) Number of anagenetic dispersal events, i.e., occurring along branches of the tree and not associated with speciation/branching events. B) Number of cladogenetic dispersals, i.e., founder events in which a lineage dispersed to an area outside the range of the ancestral nodes at speciation.

A) Dispersal events



B) Founder events



CHAPTER FIVE

Linking historical and ecological biogeography to explain the evolution of lemur diversity

Abstract

Deep time biogeographic events affect the regional pool of potentially co-occurring species at broad scales, while species interactions and environmental constraints further shape the composition of local communities. Linking the interactions between historical and ecological biogeography will elucidate the causes of species diversity and distribution. Madagascar is renowned for its super-diverse endemic biota, but the mechanisms responsible for that diversity are unclear. Most research has focused on the phylogeographic patterns of clades as well as the taxonomic composition of communities, especially lemurs. The phylogenetic and functional composition of communities has not been examined in light of biogeographic hypotheses. I compiled a geographic information systems database of environmental variables, protected areas, bioregions, and lemur species distributions to generate community matrices at regional levels for extinct and extant lemurs, and 50 local communities of extant taxa. Phylogenetic dissimilarity among communities was best explained by dissimilarity in plant productivity. The geographic structure in phylo-beta diversity strongly supports a primary division among ecoregions as well as substructure related to river barriers. Regional taxonomic, phylogenetic and functional community diversity changed in the northwest and central highlands from pre-mass extinction assemblages to the present. Pre-mass extinction regions were more species rich, the relatedness of co-occurring species did not differ from null expectations, and functional diversity was higher than modern communities. Modern communities were phylogenetically clustered in the northwestern, suggesting a subset of closely related species passed through the extinction filter. Functional trait diversity also decreased post-mass extinction. The present local community structure was best explained by primary plant productivity and the area of communities;

geographically larger communities with high plant productivity were phylogenetically overdispersed, had high species richness and high functional diversity. The results strongly support the ecoregional and river barrier hypothesis for lemur evolution and earlier arguments that emphasized the interactions of biotic and abiotic factors affecting biodiversity evolution.

Keywords: regional species pool, phylogenetic community structure, species richness

Introduction

The geographic patterns of species distributions reflect ecological and evolutionary processes driving the distribution and the diversity of life (Willig et al. 2003). Ecological biogeography focuses on recent causes of patterns in species richness and species distributions based on niche theory, environmental factors related to habitat suitability, and biotic interactions (e.g., Peterson 2011). Focusing on taxonomic richness is not informative about evolutionary time scales, however, and the phylogenetic similarity among co-occurring species and among localities is informative to make inferences about macroevolution from macroecology (Bryant et al. 2008; Wiens 2012). The geographic and temporal scales at which processes of speciation and extinction related to historical events give way to niche processes is also informative for understanding which factors are affecting diversity at each scale (Swenson et al. 2006). The forefront of biogeography is in the union of phylogenetics and ecological biogeography, linking ultimate outcomes related to lineage diversification dynamics and proximal ecological causes (Graham and Fine 2008; Price et al. 2014; Wiens and Donoghue 2004).

Links between biogeography and community ecology for explaining evolution

Biogeographic events shape the regional species pools from which local communities are assembled (Mittelbach and Schemske 2015). Local communities are then further modified by environmental filtering and competitive interactions with sympatric species (Cavender-Bares et al. 2009; Webb et al. 2002). The intersection of biogeographic fields links broad-scale processes acting on evolutionary timescales that shape regional species pools with the ecological processes that assemble local communities from regional pools (Wiens and Graham 2005 Figure 5.1). One initiative to merge historical and ecological biogeography is the concept of phylogenetic community ecology (Webb et al. 2002). A holistic community ecology quantifies the species, evolutionary, and functional diversity to elucidate causes of local community assembly from a regional species pool (Cavender-Bares et al. 2009; Graham et al. 2014; Graham et al. 2009; Pinto-Sánchez et al. 2014; Vamosi et al. 2009; Weinstein et al. 2014; Wiens 2012).

A prominent framework explaining species richness patterns is the ecological limits hypothesis, which predicts that species richness is limited by a resource-based carrying capacity (Rabosky and Hurlbert in press). Ecological limits predict that speciation is diversity-dependent; speciation rates decrease and/or extinction rates increase as total species richness increases because niches are filling and competition is increasing. If communities are limited by competition, then low resource communities should have lower species richness than high resource communities. Confirming this prediction, primary productivity is one of the strongest predictors of broad-scale patterns in species diversity (Hawkins et al. 2003). From an evolutionary framework, however, the same patterns can be explained by longer time-for-speciation, phylogenetic niche conservatism, and higher diversification rates in higher productivity habitats (Harmon and Harrison in press). This example illustrates how the evolutionary dimension of biodiversity can clarify alternate hypotheses of species accumulation.

Historical and ecological biogeography on Madagascar

The biodiversity of Madagascar has been shaped by dramatic landscape changes in the deep and recent past (Samonds et al. 2013; Vences 2009; Wells 2003). The competing hypotheses of evolutionary processes driving speciation center on the relative roles of dispersal barriers, vicariance events, and ecological diversification related to habitat suitability and niche partitioning (Vences 2009). These hypotheses have been based on a variety of methods including lemur phylogeography (Pastorini et al. 2003; Yoder and Heckman 2006), the fit of species distributions to areas of endemism and dispersal barriers (Goodman and Ganzhorn 2004b; Pearson and Raxworthy 2009; Wilmé et al. 2006), the clustering of communities based on taxonomic composition (Ganzhorn et al. 1999; Kamilar 2009; Muldoon and Goodman 2010), climatic niche divergence among closely related species (Kamilar and Muldoon 2010), and habitat-suitability models (Blair et al. 2013). The hypotheses have not been tested using the phylogenetic or functional relatedness of species in communities. As illustrated below, each biogeographic hypothesis suggests explicit patterns of the taxonomic, phylogenetic and functional similarity of the species that make up communities, and offers a new framework to test old hypotheses about biogeographic evolution on Madagascar.

***Ecoregions hypothesis*:** Madagascar is characterized by the wet east coast and steeply sloping mountain chain, transitioning westward to the central high plateau, a mosaic of largely anthropogenic landscape and high montane grass and woodlands. West of the plateau are the dry deciduous forest and southern deserts. The clustering of eastern versus western lemur communities based on taxonomic compositions supported the assertion that the diversity in Madagascar evolved due to ecological divergence (Ganzhorn et al. 1999; Godfrey et al. 1999; Kamilar 2009; Kamilar and Muldoon 2010; Martin 1995; Martin 1972; Muldoon and Goodman 2010; Richard 1991; Tattersall 1982). The modern habitats most likely originated in the Miocene, as Madagascar reached its current latitude and the trade winds from the Indian Ocean brought warm moist air to the eastern coast (Wells 2003).

Predictions: Beta diversity patterns are predicted to reflect dispersal limitation due to climate and habitat type: strong signal of low beta diversity between similar habitats (Figure 5.2a, solid lines) and high diversity between dissimilar habitats, with a weak signal of geographic distance (Figure 5.2a, dashed lines). Regional alpha diversity patterns are predicted to reflect differential diversification dynamics among regions: high speciation rates of regional communities in harsh environments (in this case, dry forest) should exhibit phylogenetic clustering of close relatives and low trait diversity due to an initial environmental filter on adaptive traits. Phylogenetic overdispersion and high functional diversity is predicted at this level in high productivity environments (here, wet forests) because of greater ecological opportunities for niche expansion, and the effects of competition among close relatives that share similar niches. A similar pattern is expected at the local community level, where competition is predicted to be the strongest factor driving functional trait divergence.

Riverine barrier / corridor hypothesis**:** Variants of the habitat specialization model suggest that the central high plateau and the rivers originating from it were barriers to dispersal north and south, but perhaps were corridors facilitating dispersal east and west (Ganzhorn et al. 2006; Goodman and Ganzhorn 2004a; Goodman and Ganzhorn 2004b; Martin and Martin 1990; Pastorini et al. 2003; Yoder and Heckman 2006; Yoder et al. 2005). The highlands and rivers most likely formed in the Pliocene as volcanism drove the uplift of the eastern escarpment (Wells 2003).

Predictions: Beta diversity patterns are predicted to reflect dispersal limitation due to habitat and geographic distance (Figure 5.2b). Regional alpha diversity should reflect higher phylogenetic overdispersion because repeated, clade-wide allopatric speciation should result in fewer close relatives co-occurring due to geographic separation, and low trait diversity due to phylogenetic niche conservatism. Local alpha diversity is predicted to have similar patterns, with geographic distance having a stronger effect on diversity than in the ecoregions hypothesis.

***Pleistocene watershed refugia, highlands dispersal hypothesis*:** Cyclical climate change related to Pleistocene glacial events may have led to the isolation of forest refugia around lowland watersheds, while dispersal was facilitated by key mountains of the central highlands with stable riparian habitat (Wilmé et al. 2006).

Predictions: Beta diversity should reflect neo-endemism; taxonomic beta diversity should be high among pairs of geographically close communities, while phylogenetic diversity is low because turnover in community composition is due to the replacement of species by close relatives (Figure 5.2c). Geographic distance should have the strongest effects on beta diversity because more distant sites are separated by more dispersal barriers. Functional diversity is not predict to vary with environment or distance because of phylogenetic niche conservatism. Regional alpha diversity is expected to exhibit high overdispersion because close relatives are geographically isolated, taxonomic diversity should be intermediate because the repeated sundering of shared ancestral ranges leaves fewer species in each community, and functional diversity should be low reflecting niche conservatism. Local communities should exhibit high overdispersion, but with a stronger effect of geographic distance because distant sites are separated by more dispersal barriers.

Previous evidence for biogeographic hypotheses from community ecology

Evidence of ecological factors affecting lemur community composition include higher lemur species richness in wet than in dry forests (Stevens and O’Connor 2006), and this pattern is also related to concordant patterns in tree species diversity, community structuring related to competition based on functional traits, and fine-scale niche partitioning within communities and within guilds (Ganzhorn 1997; Ganzhorn 1988; Ganzhorn et al. 1997). The east *versus* west dichotomy is consistent in taxonomic beta diversity (comparing among sites, Ganzhorn et al. 1999; Kamilar 2009; Muldoon and Goodman 2010), but the phylogenetic beta diversity has yet to be examined and can lend insights into the evolutionary history of communities (Bryant et al. 2008; Graham and Fine 2008; Graham et al. 2009; Weinstein et al. 2014). The phylogenetic alpha diversity of lemur communities were mostly no different from null expectations, with some communities being overdispersed (Kamilar and Guidi 2010; Razafindratsima et al. 2013). There was no change in phylogenetic structure observed when comparing subfossil communities with extinct taxa and present-day communities, and little effect of climate in explaining variation in community structure (Razafindratsima et al. 2013). At the broad geographic scale used in previous studies of alpha diversity, overdispersion is consistent with allopatric speciation; close relatives tend not to co-occur because their populations are divided by barriers (Vamosi et al. 2009). The definition of regional species pools and local communities have measurable impacts on estimates and interpretations of alpha diversity (Graham and Fine 2008; Swenson et al. 2006; Vamosi et al. 2009), and the results of previous studies can be re-examined in this light.

In this study, I test the biogeographic factors that have been proposed to explain the diversity and distribution of lemurs in the framework of the lemur phylogeny, with explicit predictions that tease apart co-varying factors (Figure 5.2). I first examine the biogeographic evolution of lemurs from a broad-scale in deep time, the level at which speciation, extinction and dispersal should be the predominant factors. I then examine changes in community structure from broad to local scales in the recent past and present, the level at which ecological filtering and competitive exclusion should shape species distributions and diversity.

Materials & Methods

To quantify species richness patterns across Madagascar, I first assembled a database of geographic ranges, environmental variables, and previous biogeographic hypotheses. To quantify the diversity of communities within and among localities, I measured taxonomic, phylogenetic and functional alpha and beta community structure across localities. To test hypotheses of ecological factors predicting community diversity, I used matrix correlations and linear mixed models to test the effects of habitat productivity, climate, area, and geography while accounting for confounding effects such as spatial autocorrelation.

GIS database

I assembled a geographic information systems (GIS) database of lemur distributions, environmental variables and biogeographic regions from available sources. All layers used the WGS 84 decimal latitude/longitude geographic coordinate reference system unless otherwise noted. I created polygon shapefiles of five simplified bioregions of Madagascar based on previously hypothesized areas of endemism by georeferencing the map provided in Pastorini et al. (2003) in QGIS (Quantum GIS Development Team 2015), with 8 georeference points used to maximize the fit of the map to the GIS. The bioregions were central highlands (CH), north east (NE), southeast (SE), southwest (SW), northwest (NW). I obtained polygon shapefiles of extant lemur range maps from the IUCN terrestrial mammal database (http://www.iucnredlist.org/technical-documents/spatial-data, accessed 2/18/2015). I obtained polygon shapefiles of 50 protected areas (PAs) around Madagascar (Kremen et al. 2008). I modified some PA polygons from the original files, because several protected areas consisted of large continuous polygons as well as small polygons surrounding forest fragments. These smaller polygons were either merged within the larger polygon of the PA or excluded because of small size, distance from contiguous forest and lack of forest cover. I estimated the area of each PA using the *poly.areas* function in the R package *GISTools* (Brunsdon and Chen 2014; R Core Team 2014) and a UTM transformed shapefile of PAs. I also georeferenced the major river systems that have been hypothesized to be biogeographic barriers to dispersal (Wilmé et al. 2006). A map of the bioregions, PAs and rivers illustrates the distribution of these major geographic features (Figure 5.3).

I tabulated species presence/absence matrices for each protected area and region using the *intersect* function in the R package *raster* (Hijmans 2015). Presence/absence matrices were then verified against literature sources of ground-truthed surveys at the PAs (Mittermeier et al. 2010; Muldoon and Goodman 2010; Schwitzer et al. 2013) and references therein. Extinct lemurs lacked range maps and rather than attempt to build them based on the data available, I manually coded their regional presence / absence based on available literature sources (Godfrey et al. 2010; Godfrey et al. 1999). Previous studies have examined community structure with subfossil lemurs at more local scales by assuming that subfossil assemblages contained all the extant taxa of nearby present-day sites (Razafindratsima et al. 2013). I avoid this assumption here and only make inferences at the regional level. The regional and local community matrices are available in the Dryad online data repository. For the regional community matrix that included subfossil lemurs for the parametric biogeographic analysis and regional community structure analysis below, I included *Indri* and *Hapalemur simus* as occurring in the NW region; their remains have been found in subfossil assemblages in Ankarana and those populations have since gone extinct (Jungers et al. 1995).

I assembled climate and elevation layers from the WorldClim raster data layers (30 arc-second resolution, Hijmans et al. 2005) and extracted the environmental variables for each protected area. I focused on the following environmental variables because they characterize habitats well and minimize correlation among independent variables: mean annual temperature, isothermality, temperature seasonality, total annual precipitation, precipitation seasonality, precipitation of the driest quarter, and elevation. I also included a layer of primary productivity, the Normalized Difference Vegetation Index (NDVI), which was generated from the MODIS imagery of the NASA Terra satellite (http://neo.sci.gsfc.nasa.gov, accessed 3/29/2015). I compiled data layers from the month of September (roughly peak dry season) and February (peak rainy season) in the years 2010 – 2014 and calculated the mean NDVI across years to incorporate inter-annual variation. I used the *extract* function in *raster* to calculate unweighted means of environmental variables for each PA and for elevation the mean and standard deviation were calculated to quantify topographic variability as a predictor. All the data for each PA are available in the Dryad repository.

Taxa and phylogeny

I used a total evidence phylogeny that included ~90% of living and extinct lemurs (this dissertation, Chapter Two). Species that were missing from the original phylogeny (16 species) did not have comparable genetic loci to those used in the phylogenetic inference, but were proposed based on mitochondrial genetic divergence. Because comparative biological inferences are affected by missing data (Rangel et al. 2015), I grafted those missing species onto the phylogeny manually based on the relative position of missing species to their congeners as suggested from the original publications (Appendix III). The resulting complete phylogeny allowed me to include all the available local communities and regional species distributions without biasing the results due to missing taxa.

Community ecology

Beta diversity**:** I calculated the turnover in diversity between pairs of communities in terms of taxonomic and phylogenetic beta diversity. I calculated the Sorenson's and Phylo-Sorenson's dissimilarity indices, functional trait dissimilarity, environmental dissimilarity (Euclidean distance matrices of precipitation, elevation, environmental variable), and geographic distance using R packages (Appendix IV). The competing hypotheses for lemur biogeography predict different relationships between lemur community dissimilarity and environmental variables. I tested for significant relationships among taxonomic, phylogenetic and trait beta diversity, environmental dissimilarity and geographic distance using partial Mantel tests (*multi.mantel* function in *phytools*, Revell 2015). I calculated statistically similar clusters of sites based on the unweighted pair group method with arithmetic mean (UPGMA) of the phylogenetic beta dissimilarity matrix using the *upgma* function in the *phangorn* package (Schliep 2011).

Alpha diversity**:** To investigate the effects of ecological biogeography on the composition of regional and local communities, I quantified taxonomic, phylogenetic and functional trait community alpha diversity at two levels. 1) "Regional communities": five regions, with all lemur species were included in the source pool of species that could potentially occur in a region. 2) Local communities within five regions: each PA, with the species lists for each region as the source pools. These two levels were chosen to quantify large scale biogeographic processes at the regional scale (differential diversification dynamics among regions, dispersal limitation), and local processes in which species co-occurrences are more likely mitigated by interspecies interactions (competition or mutualisms) and environmental filtering (Cavender-Bares et al. 2009).

For each region and local community, I calculated taxonomic structure as the species richness, or total number of species with ranges overlapping the region/PA. I calculated phylogenetic community structure using the mean nearest taxon index (MNTD, Webb et al. 2002). MNTD is a measure of the mean pairwise branch-length distance among pairs of co-occurring taxa. To assess if MNTD differed significantly from random expectation, I compared the observed MNTD value to that expected given a null distribution from randomizing the presence/absence matrix but maintaining species prevalence (richness null model, in *picante* (Kembel et al. 2010). Negative MNTD values that fall under 0.05 percent of the null distribution were considered phylogenetically clustered, while positive MNTD values higher than 0.95 percent of the null distribution were considered phylogenetically overdispersed. I quantified functional trait diversity using Rao's quadratic entropy, a metric based on the Gower dissimilarity making it an ideal measure because it can handle data on different scales (Rao 1982) implemented in the R package *syncsa* (Debastiani and Pillar 2012). The functional traits used to calculate Rao's quadratic entropy were compiled from the literature, and were chosen to represent fundamental aspects of niche dimensions. These included: 1) body size (natural log, grams), 2) diet category, and 3) activity pattern (Appendix IV). I calculated these metrics at the regional level with both the extant-only and the extinct taxa to examine if the alpha diversity in regional communities changed with the extinction of the giant lemurs.

Because of small sample size at the regional level (only five regions), community structure metrics were compared qualitatively. At the local community level (50 PAs), I tested for correlations among community structure metrics. These metrics are highly positively correlated (Appendix IV), suggesting they are each measuring aspects of community structure. I therefore used multivariate multiple regression, testing the effects of fixed factors on the linear combination of the three dependent variables. I used linear mixed models (lmms using the *nlme* package (Pinheiro et al. 2011) in R. In these analyses, geographic region was included as the grouping factor, environmental variables were fixed factors, and a geographic distance matrix was included in the error structure to control for spatial autocorrelation (Appendix IV).

Results

Beta diversity

Phylogenetic, taxonomic, and functional beta diversity were positively related (Mantel test, phylo-taxonomic: $r=0.57$, $p<0.001$, $r^2=0.63$, phylo-functional: $r=0.52$, $p<0.001$, $r^2=0.57$, functional-taxonomic, $r=0.90$, $p<0.001$, $r^2=0.87$). Residual phylo-beta diversity, after controlling for taxonomic beta diversity, was best predicted by dissimilarity in dry season NDVI ($r = 0.03$, $t = 9.38$, $p<0.001$) and geographic distance ($r = -0.01$, $t=-4.87$, $p<0.001$, Appendix IV). Residual phylo-beta diversity was related to precipitation and altitude dissimilarity in partial Mantel tests without NDVI, but those variables are nonsignificant in tests that include NDVI (Appendix IV). There was greater phylogenetic diversity than expected given taxonomic diversity with greater dissimilarity in primary productivity. Residual functional beta diversity, after controlling for the correlation of functional and phylogenetic beta diversity, was predicted by NDVI dissimilarity ($r=0.03$, $t=9.19$, $p<0.001$) and geographic distance ($r=-0.01$, $t=-5.41$, $p<0.001$), but not elevation or precipitation dissimilarity ($r<0.01$, $p>0.05$). The results suggest that taxonomic, phylogenetic and functional dissimilarities among PAs are independently affected most by primary plant productivity and geographic proximity.

The results suggest strong phylogenetic structuring due to habitat, and weak effects of geographic distance. 12.5% of pairwise site comparisons have residual phylogenetic beta diversity lower than expected given taxonomic diversity (residual phylo-beta diversity < -0.1); 12.7% have greater phylo-beta diversity than expected (residual phylo-beta diversity >0.10).

Clear geographic structure was apparent when the phylo-beta diversity was depicted as a UPGMA dendrogram (Figure 5.4). The east / west dichotomy was evident; eastern PAs clustered together to the exclusion of western PAs. The NE and SE regions formed a cluster with most NW PAs to the exclusion of a cluster composed of SW and three NW PAs. The NW and SW region PAs clustered to the exclusion of each other, suggesting the Tsiribihina river was a barrier between them, with the exception of three NW PAs that clustered with the SW. The separation of NE and SE PAs corresponded with the Mangoro river, and subdivisions within NW and SW were coincident with proposed river barriers (the Betsiboka river in NW, Manampatrana in SE, and Onilahy in SW).

Regional alpha diversity

Extant species richness was highest in the NW (49 species), and the NW was phylogenetically clustered (MNTD = -1.49, p = 0.057, Table 5.1). Species richness was also high in the CH region (34 species), which was phylogenetically overdispersed (MNTD = 1.50, p=0.921). The other regions had positive MNTD values, but did not differ significantly from the null expectation based on community matrix randomization. Functional trait diversity tracked phylogenetic diversity; Rao’s quadratic entropy was highest in CH, NE, and SE (~0.82), while diversity was lower in NW and SW (~0.77, Table 5.1). These results support the observations from the historical biogeography analysis of high within-region cladogenesis (exact range inheritance), particularly for the NW region, where ancestral range inferences suggested many subclades originating within that region, reflected in the high prevalence of closely relative species with similar traits and thus, phylogenetic clustering and low trait diversity.

The regional alpha diversity including the extinct taxa suggests that all regions were no different from the null model in the pre-extinction Holocene, and functional diversity was similarly high in all regions (Rao ~ 0.86, Table 5.2). These results suggest that the regional community diversity of Madagascar did change post-extinction, especially in the CH, NW and SW where extinct taxa once expanded the diversity and functional niche space compared to present regional communities. The post-extinction clustering observed in the NW should then be interpreted as a limited subset of closely related taxa with low trait diversity passing through the extinction filter.

Within-region alpha diversity

Local communities within regions were either not significantly different from the null expectation (46%) or were phylogenetically overdispersion (54%, Appendix IV). There were significantly more overdispersed communities within regions than non-overdispersed communities (χ^2=17.54, p <0.001, test on the number of overdispersed *versus* null communities in the five regions). This prevalence of overdispersion held for all regions except SW in which no communities differed from the null expectation at the $\alpha_{\text{one-tailed}}$ level of 0.05 (n=11 communities; four communities were overdispersed at $\alpha_{\text{one-tailed}}$=0.10). Phylogenetic structure was positively related to (natural log) species richness (t_{44}=3.56, p<0.001) and functional trait diversity (t_{44}=2.83, p<0.01), and functional diversity was positively related to (natural log) species richness (t_{44}=15.29, p < 0.001). The covariation among community structure variables thus warranted the multivariate regression approach to summarize the diversity metrics into a linear combination of community structure.

Alpha diversity and environmental variables

The strongest predictors of community structure were the primary plant productivity in the dry season and PA area (Figure 5.5, Table 5.3). Mean annual temperature and annual rainfall were significant predictors of community structure individually and in combination, but had nonsignificant effects on community structure once the effect of plant productivity was accounted for, suggesting their shared effects with plant productivity (Table 5.3).

Discussion

In this study, I found that phylogenetic beta diversity was higher than expected given taxonomic diversity among geographically close communities, suggesting some close localities contain relatively old endemics. Increasing phylogenetic dissimilarity among communities is best explained by increasing dissimilarity in plant productivity. I found strong support for competitive exclusion as a causal mechanism of local community assembly. The most taxonomically, phylogenetically and functionally diverse communities occurred in localities with the highest plant productivity, especially dry-season productivity, suggesting low dry-season productivity limits community diversity. Other factors co-varied with this pattern: a positive relationship between community structure, rainfall and longitude, and a negative relationship with temperature. There was also a strong effect of PA area, suggesting larger areas do support higher diversity. The results suggest that differential diversification dynamics among regions as well as habitat structuring explain the geographic distribution of lemurs.

Implications of phylogenetic community ecology for biogeographic hypothesis in Madagascar

The biogeographic causes of species distributions in Madagascar, especially areas of high microendemism, have been the subject of great debate. The gradients in rainfall from east to west and north to south create distinct biological domains, partially due to the orography of the eastern mountain chain (Wells 2003). Patterns of some species' distributions correspond to different domains or climatic niches, suggesting ecological adaptation driving species differentiation (e.g., Blair et al. 2012, Kamilar and Muldoon, 2010, Pastorini et al. 2003, Pearson and Raxworthy 2009). The taxonomic beta diversity of sites recovers the east/west divide (Kamilar 2009, Ganzhorn and Wright 1999, Muldoon and Goodman 2010, Godfrey et al. 1999). Within domains, several key rivers have also been hypothesized to act as barriers to dispersal (Martin 1996, Pastorini et al. 2001). These bioregions and riverine barriers were supported as key factors structuring the geographic distribution of species.

Combining the taxonomic and phylogenetic beta diversity of communities can elucidate the evolutionary and temporal dimensions of geographic structure in diversity (Graham and Fine 2008). I found that pairs of communities that were more phylogenetically dissimilar than expected given their taxonomic beta diversity had greater dissimilarity in plant productivity, supporting the role of ecological factors in shaping species co-occurrence, as observed for alpha diversity. Functional beta diversity was related to habitat dissimilarity independent of phylo-beta diversity, rejecting phylogenetic niche conservatism as a process that drives the habitat structuring observed in phylo-beta diversity, and supporting the hypothesis that species have functional adaptive traits to their environments (Pyron et al. 2014, Wiens et al. 2004). The strong effect of habitat dissimilarity on lemur phylogenetic dissimilarity and weak but significant effect of higher phylogenetic dissimilarity among geographically close sites supports a mixed model of ecoregions and possibly recent geographic dispersal limitation structuring the phylogenetic, taxonomic and functional diversity of lemur communities.

The phylogenetic structure of lemur beta diversity supports the ecoregion and riverine barrier hypotheses; sites within each region clustered together independent of *a priori* regional classification. Four central highland communities clustered with eastern communities, and three northwestern communities clustered with those in the southwest, as might be expected with some limited dispersal among regions. Previous analyses of Madagascar taxonomic beta diversity recovered the east-west divide, but no further subdivision was apparent, especially within the eastern region (Muldoon and Goodman 2010, Kamilar 2009). In contrast, I found that several rivers do seem to divide the phylogenetic beta diversity within regions. The border between the NW and SW regions is based on the Tsiribihina river, and the Mangoro separates the NE and SE (Martin 1999). Each of these rivers appears to have acted as a barrier based on the clear structuring of communities north and south of them. Within these broad regions, sub-structuring was observed that could be attributed to the Betsiboka river subdividing the NW, the Manampatrana in SE and the Onilahy in the SW. This is the first evidence to support the ecoregion and river barrier hypothesis based on the phylogenetic history of a large clade that contains many widespread species. The clear structuring of phylogenetic diversity is strong evidence that these geographic features played an important role in lemur evolution.

Effects of mass extinction on community composition

I found that the pre-mass extinction regional lemur assemblages were different from extant regional diversity. The phylogenetic structure of regions did not differ from null expectation and had high trait diversity in the pre-extinction Holocene, while the present day NW region was significantly phylogenetically clustered with low trait diversity and CH and NE were overdispersed. The NW had the highest species richness in both time periods, and the cause of post-extinction clustering is attributable to high species richness concentrated in the genera *Lepilemur, Microcebus, Avahi* and *Propithecus.* The phylogenetic clustering in the NW was coupled with low trait diversity, supporting the assertion that a limited subset of species with similar niches had higher speciation there, *or* that they shared traits that allowed them to pass through the extinction filter. The CH and NE regions were overdispersed with high trait diversity, suggesting within-region allopatry. My results differed from those of previous analyses of phylogenetic alpha community structure in Madagascar, which found that communities were mostly no different from the null expectation or phylogenetically overdispersed (Kamilar and Guidi 2010), and found no difference between pre- and post- extinction community structure (Razafindratsima et al. 2013). I argue that the difference among studies is due to differences in the spatial scale and definition of the regional species pool. Scale has an important impact in analyses of phylogenetic alpha community structure, necessitating careful consideration of the regional species pool (e.g., Swenson et al. 2007). Previous studies used all lemur species as the regional species pool, or all eastern and all western species, and local communities of sites similar to the within-region analyses in this study. A broadly defined regional pool and narrowly defined local communities may make an unrealistic assumption of possible community assemblage. Biogeographic barriers may prevent some species, e.g., *Lemur catta*, from potentially colonizing local communities outside their endemic regions, e.g., in the NE region; thus, including them in the NE regional pool for local communities may be inappropriate. In this study, I inferred the regional community structure from the source pool of all species, and the within-region local community structure from the source pool of only species actually in each region. The result is a geographically partitioned view that sheds light on the potential causes of lemur community assembly.

Local community assembly

I found that phylogenetic overdispersion was correlated with high trait diversity and species richness, suggesting competitive exclusion structures species co-occurrence at local levels within regions. These correlated aspects of community structure were positively related to primary plant productivity. The results support the hypothesis that interspecific competition structured community assembly, and that the most permissive environments with the highest plant productivity provided a resource base large enough to support high diversity. The results expand on earlier hypotheses that found dry forests had lower species richness than wet forests, related to a similar pattern in tree species richness (Ganzhorn et al. 1997). The high functional trait diversity also supports the hypothesis that communities are structured by competitive interactions (Ganzhorn 1997). These results are similar to the patterns observed in lowland hummingbirds, which were phylogenetically overdispersed in warm wet communities, while high Andean hummingbird communities were phylogenetically clustered (Graham et al. 2009). In contrast to hummingbirds, however, phylogenetic clustering was not observed at the local scale, suggesting that environmental filtering is not driving the co-occurrence of close relatives with adaptive traits.

This study links the historical and ecological factors that have shaped the geographic distribution of lemur diversity to reveal deep-time events as well as effects of current climate driving the evolution of lemurs. By combining phylogenetic history, species distributions, species richness and functional diversity I was able to test the strength of support for competing biogeographic hypotheses for the evolution of the diverse endemic primates of Madagascar. Phylogenetic beta diversity is structured by ecoregions and river barriers, with a clear north / south divide as well as east / west (Ganzhorn 2006, Heckman and Yoder 2006). Higher plant productivity in the east, related to differences in temperature and precipitation, then shaped the evolution of regional and local communities; communities with the highest productivity had the highest diversity while low productivity communities did not differ significantly from the null expectation. There were surprising exceptions to this general rule, however; in particular, Tsingy de Bemaraha in the NW had the highest phylogenetic overdispersion of all communities. Tsingy de Bemaraha and several other communities in the NW region (e.g., Tsaratanana, Mt.d'Ambre, Ankarana) had a unique mixture of wet and dry forest components (e.g., Vences et al. 2009), and had high productivity compared to other geographically close sites, and this may explain the higher than expected community diversity.

Implications for the ecological limits hypothesis

The results of this study offer a unique test of the ecological limits hypothesis. The ecological limits hypothesis predicts that carrying capacity limits species richness, and therefore areas with higher productivity (and thus carrying capacity) are predicted to have more species than lower productivity areas (Rabosky and Hurlbert 2015). Alternatively, higher productivity areas may have more species because they are areas of endemism, where species originated and have had longer time to accumulate species (Harmon and Harrison 2015). I found that primary plant productivity was the best predictor of phylogenetic beta diversity; phylogenetic dissimilarity was highest among localities with the greatest dissimilarity in productivity. High phylogenetic beta diversity, after accounting for taxonomic diversity, suggests long evolutionary time separating sites. This is concordant with the time-for-speciation hypothesis, which predicts that high productivity areas have higher species richness than low productivity areas because species have been evolving there longer, and so are expected to accumulate more species than low productivity areas.

As predicted by the ecological limits hypothesis, taxonomic alpha diversity was highest where productivity was highest. Adding the evolutionary dimension gives a more nuanced interpretation of these results, however: phylogenetic and functional diversity were also highest in high productivity areas, suggesting that co-occurring species are more distantly related and more functionally diverse than expected by chance. When communities become saturated, they accumulate species that fill similar functional niches (Petchey and Gaston 2002), yet in this system functional redundancy was low suggesting co-occurring species fill unique niches. This may suggest that even in the highest productivity sites with the highest alpha diversity, all the available niches may not be filled up.

Conclusion and conservation implications

In this study, I make strides to link the complimentary fields of historical and ecological biogeography, especially through phylogenetic community structure, to test hypotheses explaining the exceptionally diverse endemic biota of Madagascar. The results give a rich and nuanced picture of evolutionary ecology in deep time, the recent past and the present. The implications for conservation are also important; measures used to quantify biodiversity for conservation should capture the full dimensionality of taxonomic, phylogenetic and functional diversity (Purvis and Hector 2000). I found that the highest species, functional, and evolutionary diversity is generally found in the east, but I also identified exceptions that warrant special attention. These areas should be targeted for conservation efforts to preserve the multiple dimensions of unparalleled biodiversity. Further research should be conducted for other taxonomic groups in this framework, because concordance among organismal groups in their biogeographic patterns is strong evidence for a biogeographic hypothesis. Given the detailed field data that have amassed from expeditions around the island and the availability of molecular data and phylogenies for many groups, this goal can be realized.

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Tables and figures

Table 5.1.
Regional mean nearest taxon distance (MNTD) and Rao's quadratic entropy for extant species pool. MNTD is the observed minus expected values, with expected MNTD generated from randomization of the community matrix 999 times, maintaining species prevalence (richness null model).

	Species richness	**MNTD**	**P**	**Rao**
CH	34	1.38	0.91	0.81
E1	28	1.01	0.83	0.81
E2	27	0.46	0.68	0.81
NW	49	-1.45	0.08	0.80
SW	18	0.59	0.74	0.78

Table 5.2.
Regional MNTD and Rao's quadratic entropy for extinct species pool.

	Species richness	**MNTD**	**P**	**Rao**
CH	44	-0.16	0.43	0.82
NE	28	-0.35	0.37	0.81
SE	29	-0.67	0.24	0.81
NW	57	-0.79	0.22	0.82
SW	24	0.71	0.76	0.82

Table 5.3.
Results of multivariate linear mixed model regressions predicting community structure (linear combination of species richness, phylogenetic diversity, and functional diversity) from environmental variables. df = degrees of freedom. Pillai’s trace statistic is the multivariate variance remaining in the linear combination of dependent variables after controlling for variation due to independent variables.

Predictors	**Fixed factor standardized coefficient (se)**	**df**	**Fixed factor R^2**	**Pillai's trace**	**Approx. F**	**p**	**AIC**	**delta AIC**	**AIC weight**
Dry season NDVI	**0.49 (0.13)**	**44**	**0.24**	**0.43**	**11.69**	**<0.001**	**137.84**	**0**	**0.49**
Dry season NDVI PA area	0.44 (0.14) 0.15 (0.13)	43	0.26	0.51 0.31	15.70 6.74	<0.001 <0.001	138.56	0.72	0.34
Annual precipitation	0.33 (0.14)	44	0.11	0.21	4.11	0.01	140.21	2.37	0.15
Mean annual temperature	-0.26 (0.16)	44	0.07	0.14	2.48	0.07	146.61	8.77	0.01
PA area	0.27 (0.13)	44	0.07	0.39	9.72	<0.001	145.34	7.5	0.01
Altitude	0.16 (0.15)	44	0.03	0.13	2.22	0.1	148.23	10.39	0
latitude	-0.06 (0.20)	44	0.003	0.02	0.37	0.78	149.11	11.27	0
longitude	0.31 (0.16)	44	0.1	0.14	2.42	0.08	145.98	7.42	0

Figure 5.1.
Phylogenetic community ecology links historical and ecological biogeography. The processes shaping species diversity and distributions vary at different spatial scales. At the island-wide scale, diversification process related to vicariance, ecological speciation and dispersal limitation shape the regional species pool. At the regional level, environmental factors may act as filters, limiting the species that occur in local communities. At the local community scale, environmental filtering may result in communities composed of closely related species (phylogenetically clustered), while interspecies competition may limit the co-occurrence of close relatives if they share similar niches. In the local community phylogenies, tips with circles represent species present in the communities, while tips with no circles are absent. Understanding the relationships between functional traits, the environment, and potential competitors is necessary to clarify phylogenetic patterns. If functional traits are conserved among close relatives, then phylogenetic clustering should be related to low trait diversity while overdispersion should be related to high trait diversity.

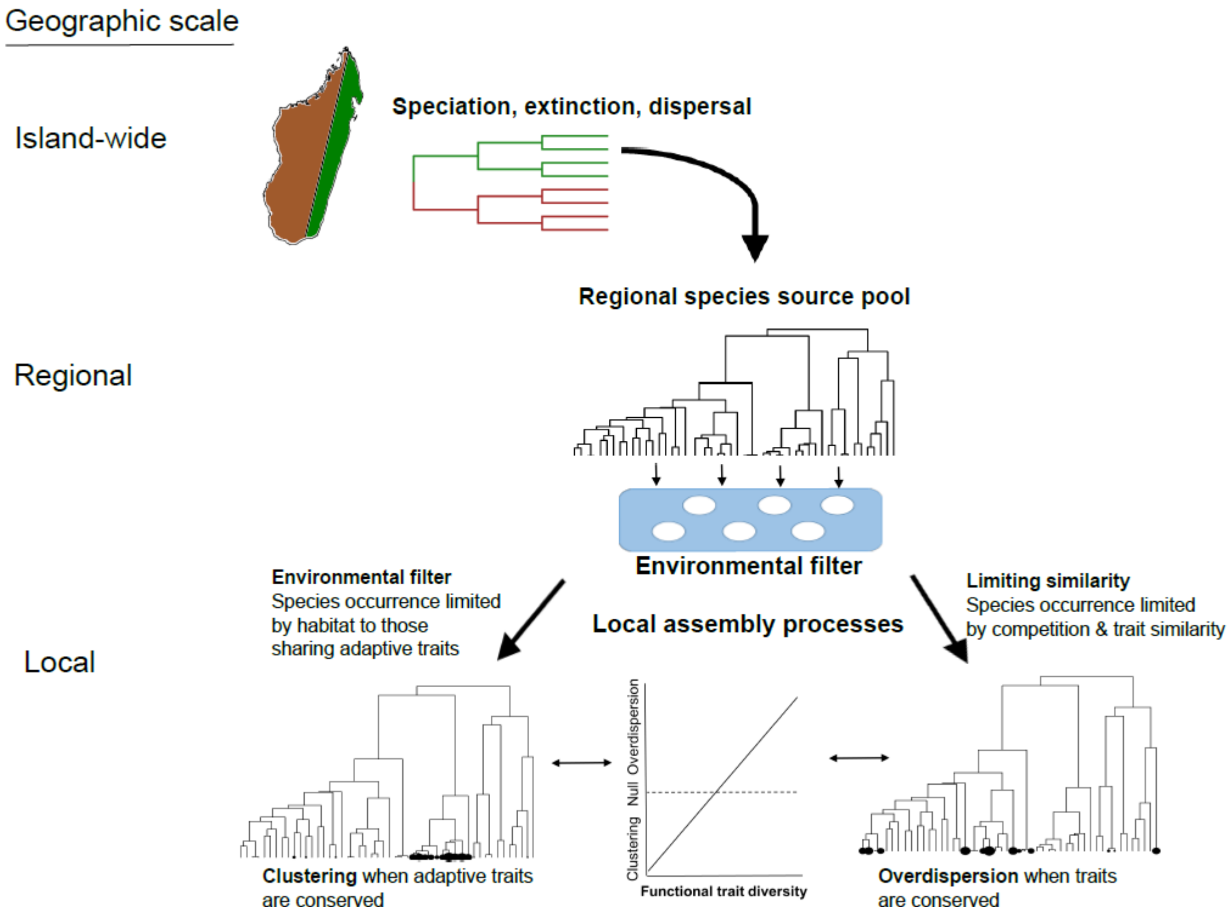


Figure 5.2.

Schematic of hypotheses and predictions. For each biogeographic hypothesis, the simplified predicted patterns of community similarity, beta diversity, regional and local alpha diversity are depicted graphically. **Ecoregions hypothesis** (A), eastern communities are predicted to have lemur communities that are phylogenetically more similar to each other than they are to western forest communities. Beta diversity patterns reflect dispersal limitation due to climate and habitat type: strong signal of low beta diversity between similar habitats (solid lines) and high diversity between dissimilar habitats, with a weak signal of geographic distance (dashed lines). Regional alpha diversity patterns reflect differential diversification dynamics among regions. In permissive environments where greater niche space is available, phylogenetic overdispersion and high functional diversity is predicted. In harsh environments where the environment filters species assembly, phylogenetic clustering and low functional and taxonomic diversity are predicted. At the local community level, competition is predicted to be the strongest factor driving phylogenetic and functional trait diversity, limited by habitat permissiveness. **River barriers hypothesis** (B), communities on the same side of a river barrier are predicted to be more phylogenetically similar than communities on opposite sides of a river. Beta diversity patterns reflect dispersal limitation due to habitat and geographic barriers. Regional alpha diversity reflects higher phylogenetic overdispersion because allopatric speciation leads to fewer close relatives co-occurring due to geographic separation, and low trait diversity due to phylogenetic niche conservatism. Local alpha diversity is predicted by geographic distance. **Pleistocene watershed refugia, highlands dispersal hypothesis** (C), communities in the same refugia regions are predicted to cluster together to the exclusion of communities in different refugia with very low dissimilarity because the branch lengths separating regions are short. Beta diversity reflects neo-endemism and geographic distance. Functional diversity does not vary with environment or distance because of phylogenetic niche conservatism. Regional alpha diversity exhibits high overdispersion, taxonomic diversity should be intermediate, and functional diversity should be low reflecting niche conservatism. Local communities should exhibit high overdispersion, but with a stronger effect of geographic distance because distant sites are separated by more dispersal barriers.

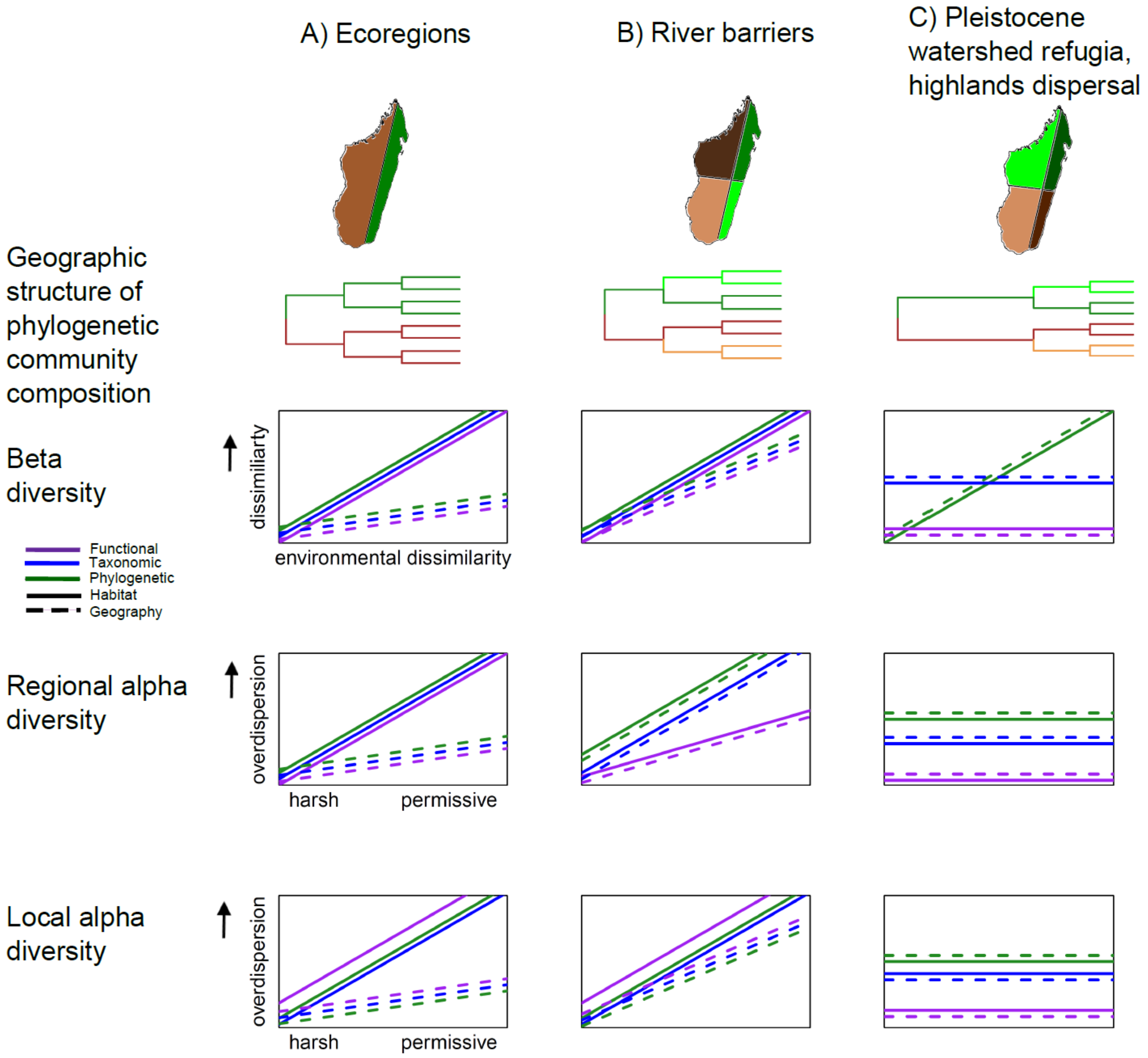
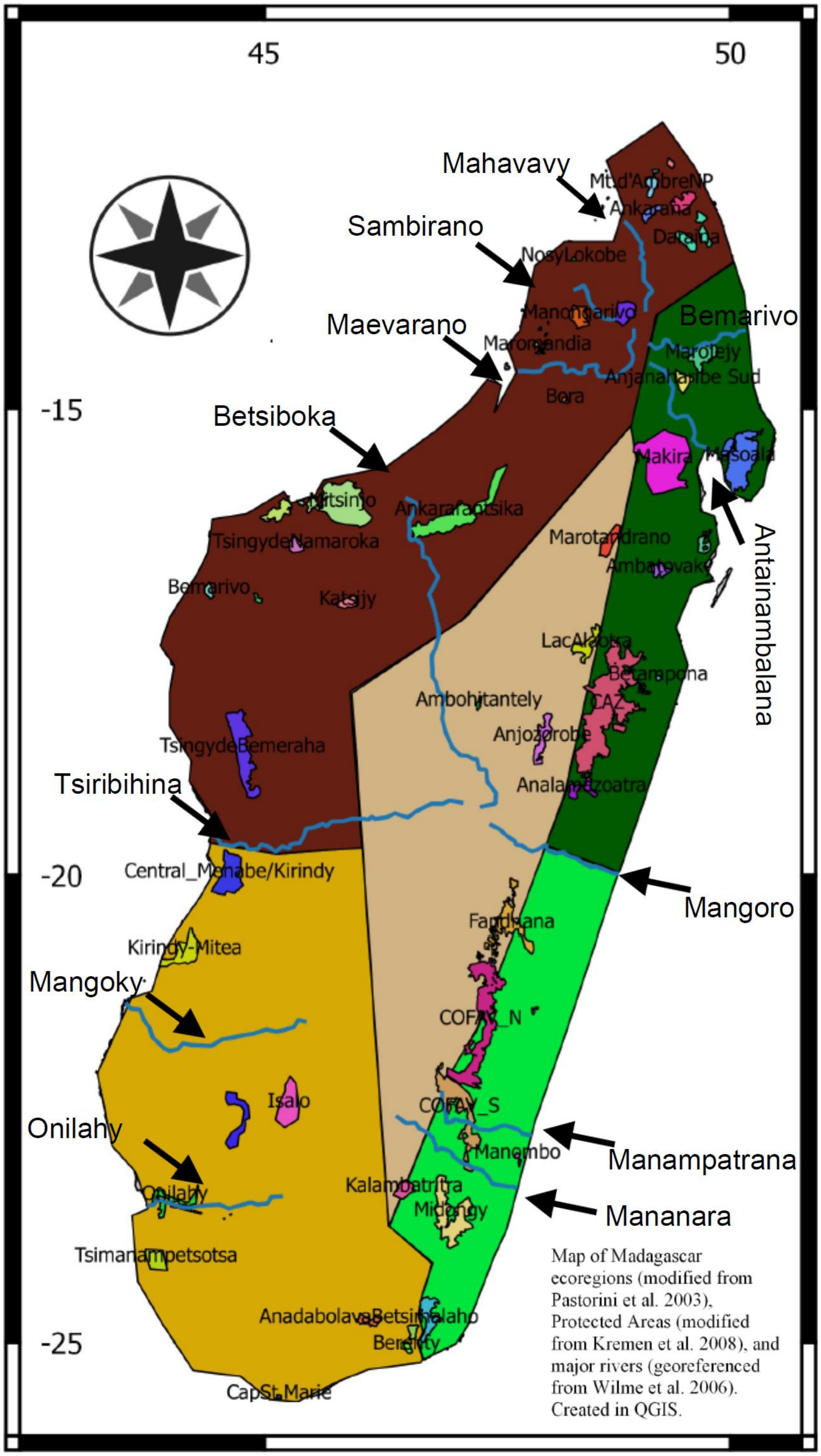

A) Ecoregions
B) River barriers
C) Pleistocene watershed refugia, highlands dispersal
Geographic structure of phylogenetic community composition
Beta diversity
dissimiliarty
environmental dissimilarity
Functional
Taxonomic
Phylogenetic
Habitat
Geography
Regional alpha diversity
overdispersion
harsh
permissive
Local alpha diversity
overdispersion
harsh
permissive

Figure 5.3.
Map of Madagascar illustrating the bioregions, protected areas, and rivers mentioned in the text.



Map of Madagascar ecoregions (modified from Pastorini et al. 2003), Protected Areas (modified from Kremen et al. 2008), and major rivers (georeferenced from Wilme et al. 2006). Created in QGIS.

Figure 5.4.

UPGMA dendrogram of phylogenetic beta diversity among PAs. Branches are color-coded for the region to which the PAs belong, based on the inset map. Clustering of PAs was based on phylo-beta dissimilarity with no *a priori* regional classifications. The geographic structure of phylo-beta diversity suggests both an east/west divide as well as north/south divisions within regions coincident with several rivers that were previously proposed to be barriers to dispersal, as indicated on the tree.

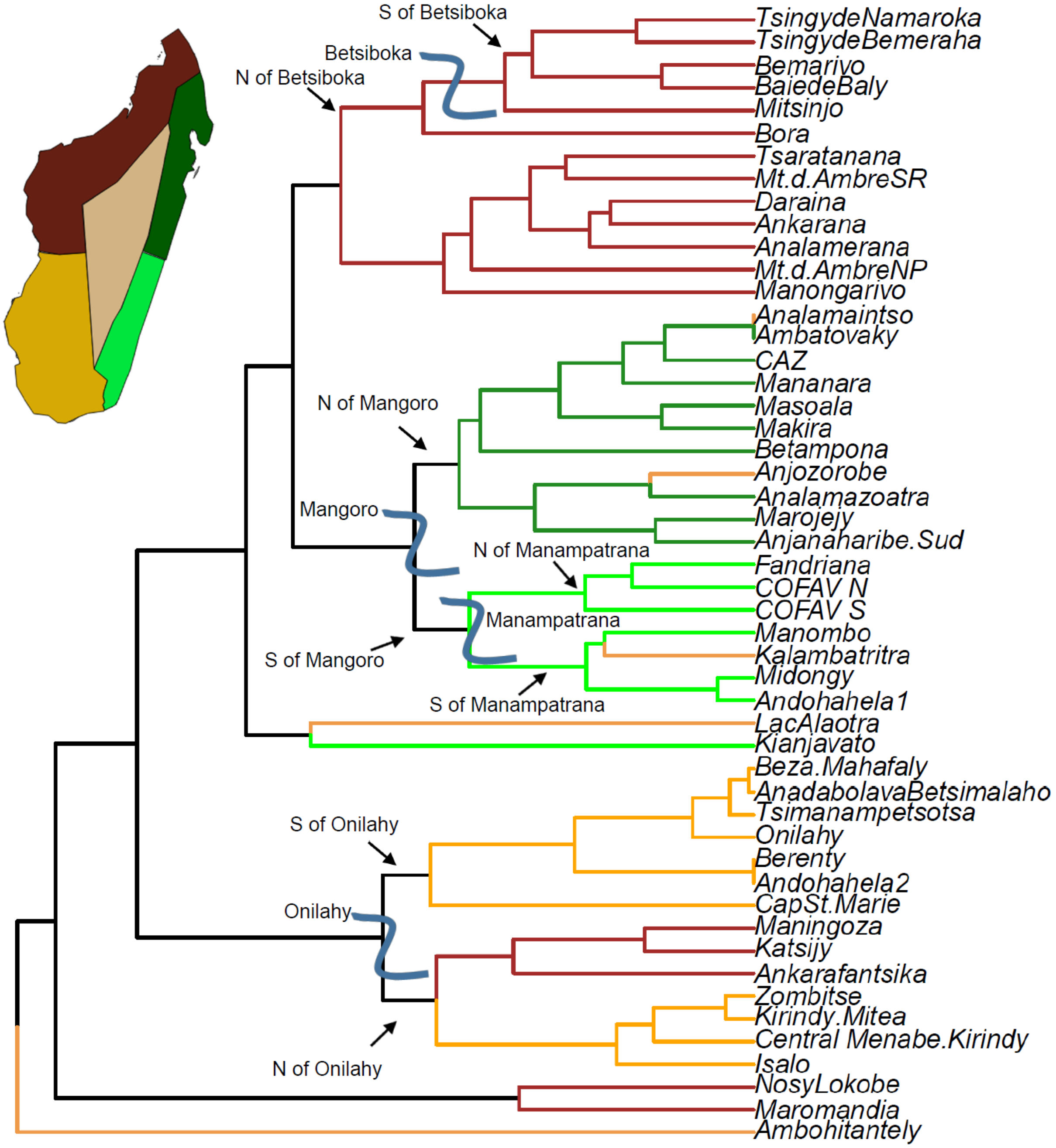
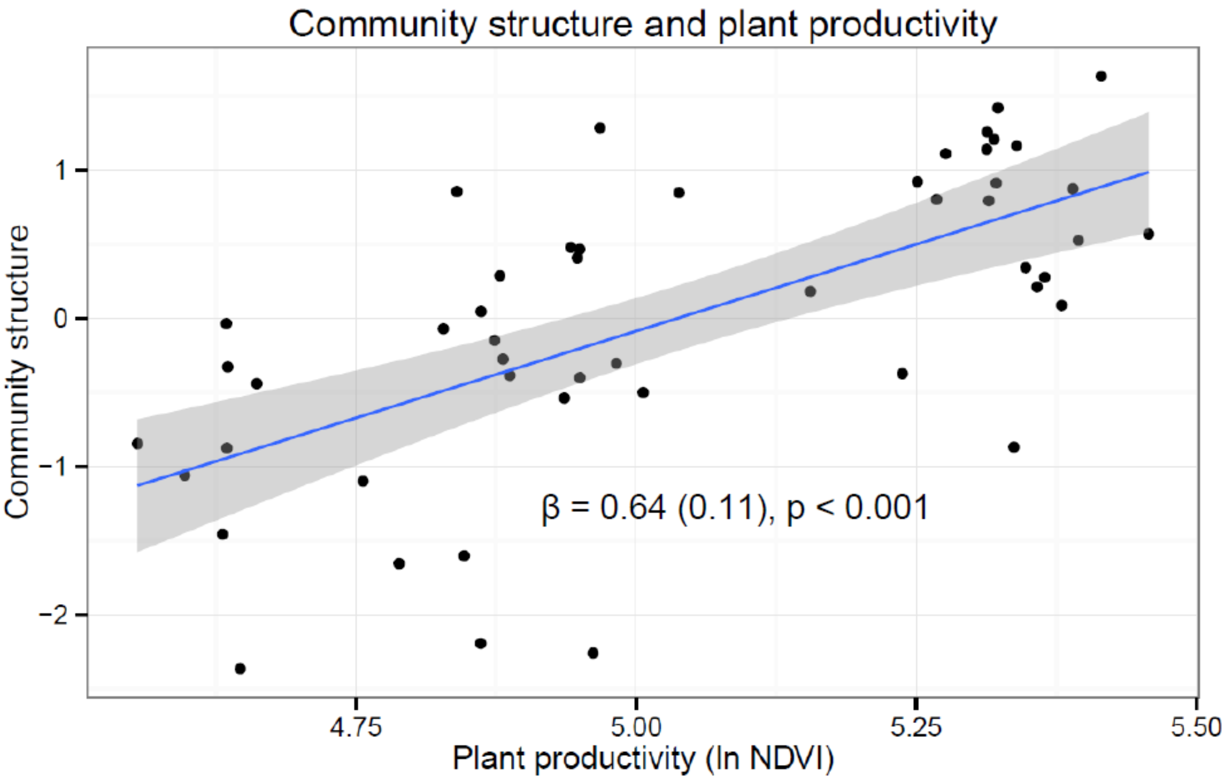


Figure 5.5.
Local community alpha diversity was best predicted by dry season primary plant productivity (NDVI). PA area was also a significant predictor, and the best models of community diversity included these two variables and explained 26% of the variation in community diversity.



CHAPTER SIX

Interactions between plants and primates shape community diversity in a rainforest in Madagascar

Abstract:

Models of ecological community assembly predict how communities may be shaped by abiotic and biotic factors. I tested how the environment, resource availability, and phenotypic traits may shape primate community assembly at local scales within one region of southeast Madagascar. I estimated the abundance of primate species along gradients of elevation, botanical composition and structure, and anthropogenic habitat disturbance. I tested the effects of habitat, phylogenetic and trait predictors on species abundances using generalized mixed models. I also tested if habitat predicts the phylogenetic and trait community structure at alpha and beta levels. I found that the abundance of closely related species was dissimilar where they co-occur, and this relationship is partially driven by trait overdispersion, indicating character displacement. Species-specific responses to elevation were the best predictors of abundance and closely related species respond differently, indicating separation along the elevation gradient. Resource abundance was the strongest predictor of community structure. High relative food tree abundance was related to phylogenetic clustering; where resources were abundant, species were closely related. High elevation communities with lower food tree abundance were phylogenetically overdispersed; species were distantly related and had low trait diversity. Functional diversity was negatively related to phylogenetic diversity; communities which consisted of close relatives were more functionally diverse than communities which consisted of distant relatives, indicating patterns of trait divergence and convergence, respectively. Integrating local scale variation in primate community composition through species abundances, evolutionary relatedness and functional diversity enlightened possible community assembly processes. I conclude that elevation and resource abundance lead to shifts in species' abundances according to phylogenetic and trait dissimilarity.

Keywords: phylogenetic community structure, phylogenetic niche conservatism, evolutionary ecology, macroecology, lemur

Introduction

Both biotic and abiotic factors affect the diversity of organisms that co-occur in ecological communities (Figure 6.1). In local communities, interspecific competition may limit the co-existence of closely related species when niches are shared from common descent (Diamond and Case 1986), leading to phylogenetic overdispersion (Webb 2000) or phylogenetic clustering when traits are divergent (Losos 2009). In contrast, species may be sorted by environmental filters, and communities may be phylogenetically clustered when co-occurring species share adaptive traits from common ancestry (Graham et al. 2009; Webb 2000), or overdispersed when traits arise via convergence (Cavender-Bares et al. 2004). Species co-occurrence may be largely stochastic, leading to a species assembly that is neutral with respect to phylogeny and traits (Hubble 2005). Testing the support for these alternate hypotheses requires combined data on environmental factors as well as diversity at taxonomic, phylogenetic and functional levels (Vamosi et al. 2009; Webb et al. 2002). Underlying these hypothesis are two assumptions that are rarely tested: 1) that phylogenetic relatedness reflects niche similarity (Vamosi et al. 2009); and 2) that resources are limiting. To date, the phylogenetic relatedness of species has been used as a proxy for trait similarity, while traits themselves are less commonly available (Kraft and Ackerly 2010). Actual measurements of the resource base are rare; typically geography and climate are used as proxies for habitat suitability and resource availability. At local scales where competition is predicted to be most important in structuring communities, species' traits and resource availability should be the strongest predictors of community composition.

Community ecology of primates

Niche partitioning is important in organizing primate communities (Ganzhorn 1988; Terborgh 1983). Among primates, competitive exclusion may prevent co-existence of close relatives in the same dietary guilds (Kamilar and Ledogar 2011). Co-occurring primate species show divergence in traits such as activity pattern and social structure (Fleagle and Reed 1996; Ossi and Kamilar 2006). There is also evidence for environmental filtering; similar environments have similar taxonomic compositions and niche diversity in many cases (Kamilar 2009; Muldoon and Goodman 2010; Reed and Fleagle 1995). Resource availability may be the most important factor limiting the diversity and abundance of primates in communities, filtering species and dietary guild composition (Janson and Chapman 1999). Leaf quality, seasonality and tree diversity are significant predictors of primate biomass and diversity in Madagascar (Ganzhorn et al. 1997). Primate community ecology is still unclear, however, on the influence of gradients in resource availability on the phylogenetic and functional trait components of diversity. Understanding these factors will elucidate the processes shaping community assembly.

Phylogenetic approaches to community ecology

To quantify phylogenetic community structure, the presence/abundance of coexisting species and the phylogenetic relatedness among them can be summarized into metrics of phylogenetic diversity and compared to null models (Kraft et al. 2007). Commonly used metrics may have limited statistical power, however (Ives and Helmus 2011; Kraft et al. 2007). For example, the phylogenetic structure of fish community metrics were no different from null expectations, but phylogenetic similarity in species' sensitivities to environmental gradients masked an underlying effect of phylogenetic overdispersion (Helmus et al. 2007). An alternative approach uses the species co-occurrence matrix as the dependent variable directly in a generalized linear mixed model framework, in which the individual species effects, phylogenetic relatedness of species, environmental characteristics, and species' traits are modeled as predictors of species occurrence / abundance (PGLMMs, Ives and Helmus 2011). Rather than assume the phylogeny is a proxy for trait similarity, the independent effects of traits can be tested.

I integrated measures of diversity in phylogeny, phenotype, and habitat to test hypotheses of community assembly 'rules' with primates from Madagascar. These endemic primates, known as lemurs, are taxonomically and phenotypically diverse. Lemurs as a clade are diverse, with 99 recognized species and some communities with >14 species living in sympatry (Mittermeier et al. 2010; Schwitzer et al. 2013). Lemurs live in diverse habitats, and patterns of species co-occurrence vary in relation to habitat heterogeneity (Ganzhorn et al. 1997; Herrera et al. 2011; Lehman et al. 2006b). I focused on local communities within a single regional species pool to test how local variation in habitat features affects lemur phylogenetic and functional diversity. At the local scale, the variation in diversity should quantify the effects of interspecific interactions and resource abundance, and not macroevolutionary processes such as speciation, extinction and dispersal or differences in climatic environmental filters as captured at broader scales (Cavender-Bares et al. 2009; Swenson et al. 2006; Vamosi et al. 2009). I predict that environmental gradients, specifically elevation, botanical composition and structure, and anthropogenic disturbance, will affect lemur community structure (Figure 6.1).

Materials & methods:

Study location

I surveyed for lemurs at five localities in southeast Madagascar: four within Ranomafana National Park (RNP), and one in the Ambositra-Vondrozo corridor north of RNP (Figure 6.2) between July 2011 and August 2014. The regional species pool consists of 12 or 13 species (Mittermeier et al. 2010), but their local occurrence and abundance varies widely, most likely due to high habitat heterogeneity (Herrera et al. 2011; Wright et al. 2012). I chose to work within this single regional pool to examine variation at a local scale, allowing me to test the predictions about density-dependent interactions within and among species and the effects of resources and environmental gradients, while limiting the effects of dispersal limitation, vicariance and extinction (Swenson et al. 2006). Defining the pool of potentially occurring species can heavily skew the results of phylogenetic community analyses (Vamosi et al. 2009). By working within this single region, the regional species pool is well defined by the species known to occur in this region. Each locality was sampled over an area of 3 – 10 km^2 using a grid of three to eight transects (1-3km long), placed according to a stratified-random design to ensure representative sampling of habitat heterogeneity (Figure 6.2, Thomas et al. 2010). In each locality, transects were between 0.5 and 1km apart approximating parallel distributions where possible.

Study authorizations: My research was approved by the Stony Brook University IACUC (2011-1875 - R1 - OBSER – USDA), and the Madagascar National Parks and the Ministry of the Environment (#225/12/MEF/SG/DGF/DCB.SAP/SCB). Research with nonhuman primates followed the guidelines for ethical research of the American Society of Primatology.

Field data collection

Lemur sampling: I conducted lemur surveys during overlapping months among localities to reduce possible systematic bias in abundance estimates due to seasonality. Each locality was sampled during 2-3 months of each the wet and dry seasons with a team of Malagasy research assistants. I conducted diurnal and nocturnal surveys on transects using distance sampling techniques (Buckland et al. 2010), a standardized methodology for estimating primate abundance (see Appendix V, Herrera et al. 2011; Irwin et al. 2000; Johnson and Overdorff 1999; Lehman 2006). We conducted repeated surveys on each transect to increase the chances of detecting all species present in the area and gain accurate estimates of encounter rates (diurnal mean = 10 repetitions, range=5-30, nocturnal mean=5, range=2 - 30).

Environmental gradients

I recorded elevation (meters above sea level) on transects every 100m using a GPS unit. I gathered data on habitat disturbance every 100m by recording instances of disturbance including cut trees and tree stumps from logging, gold mining, animal traps, forest encampments, agricultural activity, and finally human use and occupation history (Appendix V).

I measured the botanical composition and structure every 100m on each transect using the point-centered-quarter method (Appendix V, Ganzhorn 2011). Trees were identified by a team of four Malagasy research assistants trained in botany by CVB, the Missouri Botanical Garden, previous international research teams, and Malagasy forestry departments. Taxonomy was recorded as Malagasy name in the field and later translated to taxonomic Family, Genus and, where possible, species based on the extensive botanical database available at CVB. DBH was recorded with a measuring tape, while height, crown height and crown diameter were estimated by eye. Crown height was defined as the height from the first branches of the crown to the top of the tree. Crown diameter was defined as the maximum distance spanned by the branches of the tree. At each point the presence or absence of *Bakarella* sp., a hemi-parasite that grows on tree branches, was recorded because it is a known food resource for several lemurs (Arrigo-Nelson 2006; Atsalis 2007).

I tabulated the botanical data into transect X species richness and frequency for all trees, as well as the mean DBH, height, crown height and crown diameter of trees > 25cm DBH per transect. I calculated the relative frequency of lemur food trees on transects as the proportion of food trees present out of all trees recorded on each transect, plus the proportion of points in which *Bakarella* sp. was present. Lemur food trees were classified based on extensive field observations on six of the lemurs in the community (Arrigo-Nelson 2006; Balko 1998; Faulkner and Lehman 2006; Grassi 2001; Razafindratsima et al. 2014; Wright et al. 2011). The tree diversity was calculated as the Shannon-Weiner diversity index using all trees sampled on each transect. The forest structure variables were summarized using principle component analysis and the first principle component was retained as the forest structure metric for downstream analyses (summarized 70% of variation and positively related to all variables, Appendix V).

Traits

I incorporated data on traits hypothesized to be adaptations to conserve energy and maximize resource extraction in the comparatively harsh environments of Madagascar (Wright 1999): (1) social group size, (2) % leaves in diet, (3) life-history (age at first reproduction), (4) body mass (ln transformed, Appendix V). These data were gathered from primary literature and my own field work.

Data processing and analysis

Lemur abundance: I estimated lemur density (#individuals/km^2) for each species on each transect using distance sampling statistics (program DISTANCE, Thomas et al. 2010, Appendix V).

*Phylogeny***:** I used the most complete primate phylogeny published to date, combining multiple mitochondrial and nuclear loci (>60kbps) and containing all the species in the regional species pool (Springer et al. 2012). I pruned the tree to only include the species known to occur in the region (13 species).

Phylogenetic structure metrics: I measured phylogenetic diversity using two indices: 1) the mean pairwise distance (MPD), which is a metric of the summed branch-lengths separating all pairs of species in a sample; 2) the mean nearest taxon distance (MNTD), a metric of the summed branch-lengths between nearest phylogenetic neighbors in a community (after Webb 2000, implemented in the *picante* package, Kembel et al. 2010 for R, R Core Team 2014). These observed values were compared to the "frequency" null model, in which the species occurrence frequency across sites was maintained but the abundance of each species across localities was randomized (Kembel et al. 2010). The difference between the observed and expected values is the effect size of phylogenetic diversity. The sign of the values indicate phylogenetic clustering (-) or overdispersion (+), while the magnitude reflects the divergence from random expectation (random = 0). I calculated these metrics for each transect, weighting the community composition by species abundance. The data were randomized 999 times to calculate the MPD/MNTD null distributions and the observed values were significant if they were outside the 95% null distribution.

Functional diversity: I calculated the functional trait diversity of communities on transects using Rao's quadratic entropy (Rao 1982) which measures diversity as the dissimilarity among species traits, weighted by their phylogenetic relatedness and their relative abundance, ranging from 0 = species in communities have exactly the same traits, to 1 = species in communities are maximally different in their traits (*syncsa* package, Debastiani and Pillar 2012, in R).

Quantifying effects of environmental gradients on phylogenetic structure and functional diversity: To test my predictions about the effects of environmental variables on phylogenetic and trait community structure, I used linear mixed modeling (lmm using the *lme* function in the nlme package in R, Pinheiro et al. 2011).

*Phylogenetic community structure**:*** I tested the effects of each of the following independent variables alone and in combination on the phylogenetic alpha diversity metrics MPD and MNTD using lmm: elevation, botanical diversity, the relative frequency of lemur food trees, forest structure, and disturbance category. I include locality as a random effect in the models to control for within-locality variation. I also tested if models including spatial autocorrelation in the error structure significantly improve the fit to the data, based on sample-size corrected Akaike information criterion (AICc) scores (see Appendix V for quantifying spatial autocorrelation). I found the model of variables that best explained the variation in phylogenetic alpha diversity based on likelihood ratio tests between nested models, and the differences in AICc scores and weights (following Burnham and Anderson 2002).

Phylogenetic linear mixed models: The approach discussed thus far tests the effects of environmental predictor variables on a dependent variable that summarizes the species-by-site matrix and phylogeny or traits into a single value. As an alternative approach, I used mixed models to test the effects of environmental predictors, species-specific sensitivities to predictors, phylogenetic relatedness, and trait similarity on species' abundances directly (Ives and Helmus 2011). In this approach, each species' abundance on each transect serves as a dependent data point, environmental factors are fixed independent variables, and the following are random effects: species identity, species-specific sensitivity to environmental factors, phylogenetic relatedness, trait similarity, and spatial autocorrelation. Each random effect factor is a matrix that is associated with a variance scalar indicating the size of the factor's effect on species' abundances. I tested the probability of the environmental fixed coefficients being different from zero, and calculated the variance scalar with 95% confidence intervals for each random factor using the communityPGLMM function in the *pez* package of R (Pearse et al. 2015). The best model was the one with the lowest AIC.

Simulations: Previous studies have tested the power of community phylogenetic metrics to detect phylogenetic structure (Kraft et al. 2007), but did not address the following two questions: 1) What is the power of the comparisons to null distributions with very small regional and community species pools (<10 species), and 2) Does weighting community data by abundance affect power? To test the power of the MPD and MNTD metrics as well as PGLMMs to detect significant deviations from null expectations in phylogenetic community structure with different species sample sizes, I designed a simulation experiment (Appendix V). I determined the power of the metric effect sizes as the percentage of communities that were significantly phylogenetically clustered or overdispersed at $\alpha = 0.05$. I determine the false-positive rate as the percentage of random communities that were either clustered or overdispersed. For comparison, I conducted PGLMMs on these data and quantified the phylogenetic covariance/dissimilarity matrix variance scalars and 95% CIs to test if these scalars are significantly different from zero.

Results:

Lemur and tree species richness

The estimated individual population density of lemur species are given in Appendix V. Eleven of the 13 species known to occur in the region were observed during surveys or their characteristic feeding signs were observed, indicating their presence. Lemur species richness ranged from 5 – 10 (median 8). During botanical surveys, 204 tree species were identified in total (n=8365 trees), and 126 species in the 25+cm DBH category (n=1564 trees). The total species richness ranged from 44 – 81 species per transect (7 – 33 for trees with DBH>25cm), and Shannon-Weiner diversity index ranged from 3.17 – 4.05 for all trees sampled (1.15 – 3.3 for trees with DBH > 25cm), suggesting strong variation in botanical composition among transects. Of the 204 tree species identified on transects, 106 were known lemur food resources. The relative frequency of lemur food trees and *Bakarella* on transects ranged from 0.52 to 0.80 (mean=0.69). Further, the forest structure variables exhibited variation across transects (Appendix V). Surprisingly, neither the Shannon diversity index nor the relative frequency of lemur foods varied significantly in relation to elevation or habitat disturbance (lmm, fixed factors = elevation + disturbance, random factor = locality, likelihood ratio test (LRT) of fixed effects vs. null model, food trees: χ^2= 0.28, p=0.96, Shannon diversity: χ^2=5.22, p=0.16).

Phylogenetic and functional community diversity

For MPD, 19% of communities (six) were significantly phylogenetically clustered and 6% (two) were significantly overdispersed ($\alpha_{\text{two-tailed}}$ = 0.05, Appendix V). In contrast, according to MNTD only 3% (one) of communities were significantly clustered and 6% were significantly overdispersed (Appendix V). The majority of the communities had MPD and MNTD values that did not differ significantly from expectations under the null model generated by randomizing the abundances within species. MPD and MNTD values were negatively related (Appendix V); the communities with the strongest and significant phylogenetic structure according to MNTD are not different from null expectation in MPD. Both MPD and MNTD had low statistical power to detect phylogenetic structure with simulated sample sizes of <25 species (see Simulation results, Appendix V), suggesting the non-significant results may be Type II errors.

Rao's quadratic entropy was negatively related to MNTD, such that communities that were phylogenetically clustered had high functional diversity, while phylogenetically overdispersed communities had low trait diversity (lmm, fixed factor: Rao's quadratic entropy t=-2.45, p=0.02, Figure 6.3). This result indicates that the closely-related species in phylogenetically clustered communities have divergent traits, while the phylogenetically overdispersed communities were dominated by a few functionally similar species with high abundance and low abundances of other taxa with unique trait values.

Effects of environmental factors on community structure

The relative frequency of lemur food trees was the single strongest predictor of lemur phylogenetic community structure (Table 6.1, Figure 6.3). Tree diversity and elevation were also significant factors. The model that included food tree frequency, tree diversity and elevation had the highest model support (Akaike weight, w=0.504), and a simpler model with only food tree frequency and elevation was the next best model (w=0.43). Other models that included disturbance, forest structure, or spatial autocorrelation differed from the best model by a delta AIC score of >7, indicating they were significantly worse models.

PGLMM: Across all models, the species-specific effects were high in explaining variation in abundance (species-specific random intercept variance = 0.90 – 1.45, Table 6.2). This parameter accounts for the differences in mean species abundance that are not due to phylogeny or measured traits. Overall, closely-related species had similar abundances, reflecting phylogenetic signal in abundance (nonnested phylogenetic similarity variance scalar = 0.28, 95% CI = 0.21-0.35). On transects, however, closely-related species had dissimilar densities; there was strong signal of phylogenetic overdispersion (nested phylogenetic dissimilarity variance = 0.28, 95% CI = 0.24-0.31). In addition to non-zero phylogenetic dissimilarity on transects, there were independent non-zero effects of trait dissimilarity for body mass, AFR and group size (trait dissimilarity variances = 0.1, 0.15 and 0.15 respectively).

When accounting for variation in abundance due to relative food tree abundance, phylogenetic and body mass repulsion had independent effects (variances = 0.25 and 0.08, respectively), indicating competition and character displacement explain variation in abundance. Elevation was the strongest environmental predictor of abundance through species-specific sensitivities to elevation (species variance = 1.35; species-slope variance = 0.24). This effect was driven by interaction effects between species and elevation; 2/11 species had significantly negative and 2 had significantly positive relationships with elevation (Appendix V), and the sensitivities to elevation were not phylogenetically inherited (phylogenetic signal in slope variance ~0). When these effects due to elevation were accounted for, there was no signal of phylogenetic clustering or overdispersion affecting species' abundances, but there was a non-zero effect of body mass repulsion (variance = 0.10, 95% CI = 0.06-0.14). After accounting for species-specific effects of elevation, relative food tree frequency had small but non-zero species-specific slope effects on abundance (slope variance = 0.08, 95% CI = 0.03-0.12) while other environmental predictors did not have strong fixed or species-specific slope effects (Table 6.2).

Simulation results

The simulation experiments suggest low power of MPD and MNTD metrics to detect phylogenetic structure against a randomization null hypothesis, even with large sample size (100 species, SI). For communities of five species or less, less than 20% that were simulated to be clustered were significantly different from the null at $\alpha = 0.05$. Only 60-70% of communities from the 100 species pool that were simulated to be clustered were significantly clustered compared to the null. MNTD and MPD had similar magnitudes and patterns of power increase with sample size, and for most comparisons, weighting by abundance increased power compared to presence/absence only. Phylogenetic overdispersion was not detected. The false positive rates were <10% in all simulated datasets, and usually ~5%. The results suggest that quantifying the effect size of phylogenetic structuring against null models is not a statistically powerful technique.

Discussion

Factors explaining variation in species' abundances

In this study, I found strong evidence that lemur community ecology is shaped by interactions with both the abiotic and biotic environment, especially elevation and food resources. Multi-level models of abundance suggested there were strong effects of phylogenetic and body mass overdispersion, including when the effects of food tree abundance were accounted for. Abundances were dissimilar among closely-related species with similar body sizes, indicating character displacement. The overwhelming effect of elevation on species' abundances and community composition was explained by species-specific interactions with elevation; closely related species had opposite relationships with elevation. After accounting for species-specific sensitivities to elevation, other environmental factors had small or negligible effects. Analyzing the factors explaining species’ abundances incorporating trait and phylogenetic similarity suggest lemur communities are structured by character displacement along elevation and body size niche axes.

Factors explaining phylogenetic and functional community structure

I found that the most significant predictor of variation in lemur phylogenetic and functional community structure was the relative frequency of lemur food trees on the study transects. Other significant predictors such as tree diversity and elevation explained unique variation in lemur community structure, while forest structure and anthropogenic disturbance did not. Functional diversity was strongly related to phylogenetic structure. Counterintuitively, the most functionally diverse communities were the most phylogenetically clustered ones; communities composed of close relatives had divergent traits. While it is commonly assumed that a phylogenetically diverse community is also diverse in niche traits (e.g., Webb 2000), this assumption is rarely tested and not often met (e.g., Cavender-Bares et al. 2009). The PGLMMs results support trait dissimilarity as a strong predictor of variation in species’ abundances. The functionally divergent communities are consistent with the hypothesis of character displacement, in which species with unique traits co-exist because they avoid competition (Losos 1996; Schluter 2000). I found strong support for this mechanism of community assembly from direct evidence of trait and phylogenetic structure. Phylogenetic structure metrics for most communities did not deviate from null expectations, but simulations have shown that these metrics may suffer from high Type II errors.

The strongest predictor of lemur community structure was the relative frequency of lemur food trees, and counter to my initial predictions, lemur communities were phylogenetically clustered where resource availability was highest and trees most diverse, while communities were overdispersed where resources were most scarce and trees less diverse. When assessing the factors that predict species' abundances, the effect of phylogenetic overdispersion was strong; phylogenetic relatedness was negatively related to species' abundances on each transect. A similar phenomenon was observed in sunfish; phylogenetic community metrics suggested clustering, but when the effects of environmental variables that caused initial clustering were accounted for, the effect of overdispersion was evident (Helmus et al. 2007). The hierarchical modelling framework allowed variation due to the underlying pattern of overdispersion to become clear when environmental filtering causes an overall effect of phylogenetic clustering.

Resource and abiotic factors affecting primate abundance

Several lines of evidence support the role of food resources in shaping primate community assembly. For example, there are strong relationships between the population density of frugivorous, seed-dispersing New World monkeys and seedling recruitment (Stevenson 2000). Further, African forest fragments lacking known seed-dispersing monkeys also had lower seedling recruitment than continuous forest with complete monkey communities (Chapman et al. 2013). The relationship is not as clear, however, within intact forests; long-term changes in population densities of African monkeys did not track changes in food resource availability, suggesting other factors such as predation or parasitism may be driving community composition (Chapman et al. 2010). More broadly, understanding the interactions among trophic levels in communities, including the phylogenetic and trait diversity of producers and consumers, can elucidate the mechanisms behind diversity. For example, although pollinator communities in one experiment were generalized, with several species visiting the flowers of many different plant species, traits related to pollinator attractiveness were phylogenetically conserved among plants leading to phylogenetic clustering of flower visitations (Rafferty and Ives 2013). Further, the availability of prey may be an environmental filter for certain predators while competition for prey may also limit the similarity of prey-preference in predators (Morlon et al. 2014). The results of this study and several others that quantify the biotic interactions among trophic levels illustrate that these interactions are important factors shaping the community assembly within trophic levels.

The small effect of spatial autocorrelation in all analyses reinforces that this study captured variation in community composition due to local phenomena such as interspecific competition, resource limitation, and habitat suitability, rather than macroecological/evolutionary forces such as dispersal limitation, speciation or extinction (Beaudrot et al. 2013; Beaudrot and Marshall 2011). By investigating phylogenetic community structure at such local scales, I observed variation in lemur phylogenetic community structure that cannot be explained by geographic isolation alone.

The history of anthropogenic habitat disturbance on transects had no significant effect on lemur community structure, alone or in combination with other variables. I predicted that habitat disturbance would act as an environmental filter, culling the species present in local communities such that only those species with traits adaptive to degraded landscapes could co-exist. The idiosyncratic sensitivities of species to disturbance observed in the PGLMMs could not be explained by phylogeny or the traits in this study. The nuanced responses of organisms, especially primates, to human habitat degradation has made generalizations about the responses of communities to disturbance difficult (Irwin et al. 2010). Similar results were suggested for lemurs in relation to the distance from the forest edge, which was not a linear predictor of differences in lemur population density, despite the pronounced effects on forest structure and composition (Lehman et al. 2006a). While some species clearly had higher population densities either near the forest edge or in the forest interior, other species showed no relationship or nonlinear relationships such that overall community structuring is not evident (Lehman et al. 2006a). These species-specific responses, as well as other factors not included in this study (e.g., predation, parasitism), may explain why anthropogenic disturbance did not have the predicted measurable effects on lemur phylogenetic community structure and may account for the residual variation in diversity and remain important variables for future investigation.

The processes hypothesized to dominate in local communities such as those surveyed in this study include the interactions of resource limitation and interspecies competition, which should lead to phylogenetic or niche divergence. Communities that were phylogenetic clustered consisted of a few sister-species pairs that had high relative abundance, and low relative abundance of other species. Once this effect of food tree abundance was statistically accounted for, the effect of phylogenetic overdispersion was clear. Recent assessments of lemur phylogenetic community structure found that many lemur communities were overdispersed across Madagascar (Kamilar and Guidi 2010; Razafindratsima et al. 2013). The recent extinction of as many as 17 species of large-bodied lemurs (Godfrey et al. 2010) was hypothesized to drive the overdispersion in modern assemblages (Kamilar and Guidi 2010), but incorporating data on recently extinct assemblages also recovered a signal of overdispersion (Razafindratsima et al. 2013). At the island-wide scale, the predominant processes should be environmental filtering (Cavender-Bares et al. 2009, Vamosi et al. 2009). The predominant signal of overdispersion could be explained by two processes. First, widespread competition may preclude lemurs filling similar niches from co-existing; each site is composed of different species that fill similar niches. The second process that could produce widespread overdispersion is frequent allopatric speciation (Vamosi et al. 2009), which has been proposed to explain the diversity and distribution of lemurs (Wilmé et al. 2006). Thus, overdispersion recovered at the island-wide scale is a surprising finding that requires integrated biogeographic and functional trait data to fully interpret.

The simulation experiments in this study corroborate earlier findings which suggested that phylogenetic metric approaches employed to test for significant phylogenetic structure is not statistically powerful. Communities that were evolved to be clustered were only detected in ~70% of simulations with the largest regional species pool (100 species). Significant overdispersion was not detected, and counter to predictions were often found to be significantly clustered. This may be due to the difficulty of detecting overdispersion using current methods. With simulated small sample sizes (10 – 15 species, similar to the empirical dataset in this study), only 20-40% of clustered communities were detected. Thus, detecting signals of overdispersion and clustering in nature via null model comparison may be especially difficult with most study systems, as reported in previous studies (Kraft et al. 2007, Helmus and Ives 2011). New methods that use phylogenetic generalized linear mixed modelling (PGLMM) may have more statistical power to detect effects of species identity and phylogenetic relatedness to test hypotheses of community structure (Helmus and Ives 2011, Rafferty and Ives 2013). Indeed, the PGLMMs performed better in detecting patterns of phylogenetic and trait effects on simulated community composition. Our results support earlier studies that suggest the PGLMM framework provides a statistically powerful, flexible approach to test nuanced hypotheses about community assembly processes.

In conclusion, this study is the first to show with field measurements of lemur abundance and resource availability that the local community dynamics of lemur assemblages was explained by variation in food resource availability and elevation. Evolutionary and functional diversity were affected by botanical composition, and varied even across small spatial scales relative to the dispersal abilities of these organisms. The results suggest that species-specific responses to elevation, overall effects of local resource availability and phylogenetic and trait dissimilarity are most important factors shaping lemur community assembly.

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Tables and figures

Table 6.1.
Summary of linear mixed model analysis of environmental factors predicting lemur phylogenetic community structure (dependent variable = MNTD). Model probability is first compared against the null model of only MNTD and the intercept using the likelihood ratio test (LRT). Model probability is then compared for multivariate models against simpler models that contain only one of the predictors using LRT. The best model explaining phylogenetic structure (last) contains the relative frequency of lemur food trees on transects, elevation and the Shannon diversity of trees.

Hypothesis	Factors	DF	Fixed factor coefficient	Fixed factor p	Model p (against null)	Model p (against simpler model)	Model R2	Model AIC	Delta AIC	Weight
Relative food tree frequency + tree diversity + elevation	Fixed: food tree	23	-0.39	0.01	0.00	0.1274	90.10	73.75	0.00	0.50
	Fixed: tree diversity	23	-0.20	0.16						
	Fixed: elevation	23	0.51	0.00						
	Random: Locality	5								
Relative food tree frequency + elevation	Fixed: food tree	24	-0.47	0.00	0.00	0.0025	89.37	74.07	0.32	0.43
	Fixed: elevation	24	0.53	0.00						
	Random: Locality	5								

Hypothesis	**Factors**	**DF**	**Fixed factor coefficient**	**Fixed factor p**	**Model p (against null)**	**Model p (against simpler model)**	**Model R2**	**Model AIC**	**Delta AIC**	**Weight**
Null model MNTD fixed + spatial autocorrelation	Fixed: -	26	-	-			62.73	88.13	14.38	0.00
	Random: -			-						
	Spatial: Ratio			-						
Null model MNTD	Fixed: -	26	-	-			87.47	83.57	9.82	0.00
	Random: Locality	5		-						
Null model MNTD mixed + spatial autocorrelation	Fixed: -	26	-	-			87.06	84.99	11.24	0.00
	Random: Locality	5		-						
	Spatial: Ratio			-						
Elevation	Fixed: elevation	25	0.38	0.05	0.07	-	87.40	82.28	8.53	0.01
	Random: Locality	5		-						

Hypothesis	Factors	DF	Fixed factor coefficient	Fixed factor p	Model p (against null)	Model p (against simpler model)	Model R2	Model AIC	Delta AIC	Weight
Tree diversity	Fixed: tree diversity	25	-0.27	0.08	0.08	-	88.05	82.05	8.30	0.01
	Random: Locality	5		-						
Tree diversity + elevation	Fixed: tree diversity	24	-0.33	0.03	0.02	0.0236	88.08	79.33	5.58	0.03
	Fixed: elevation	24	0.43	0.02						
	Random: Locality	5								
Forest structure	Fixed: forest structure	25	-0.22	0.28	0.26	-	87.95	84.30	10.55	0.00
	Random: Locality	5		-						
Habitat disturbance	Fixed: disturbance1	24	-0.37	0.57	0.63	-	87.82	86.66	12.91	0.00
	Fixed: disturbance2	24	-0.20	0.90						
	Random: Locality	5								
Relative food tree frequency	Fixed: food tree	25	-0.32	0.04	0.04	-	88.40	81.22	7.47	0.01
	Random: Locality	5								

Table 6.2.
Phylogenetic generalized linear mixed model results. For each model, the fixed factors included, fixed factor coefficients with standard errors and Akiake information criterion (AIC) are given. Phylogenetic covariance is the weight of the phylogenetic covariance matrix representing the strength of the effect of phylogenetic similarity predicting species abundance, while phylogenetic repulsion is the weight of the inverse of the phylogenetic covariance matrix representing the strength of phylogenetic dissimilarity in predicting abundance. Trait covariance and repulsion are weights for the matrices representing species similarity and dissimilarity in traits, respectively (results shown are for body mass). Species specific intercept and slope are parameters associated with the species grouping factor in the mixed model, indicating species differences in abundance not explained by other factors in the model. The best model (lowest AIC) included elevation, food tree abundance, forest structure, disturbance, body mass dissimilarity and species-specific effects.

Fixed factor	**Fixed effect Coefficient (se)**	**AIC**	**phylogenetic covariance**	**phylogenetic repulsion**	**trait covariance**	**trait repulsion**	**species-specific intercept**	**species-specific slope**
elevation + food abundance + forest structure + disturbance	-0.06 (0.15); 0.08 (0.07); -0.04 (0.11); <0.01 (<0.01)	839.67	-	-	-	0.04 (0.01,0.08)	1.29 (1.1,1.5)	0.20 (0.13,0.30); 0.08 (0.03,0.12); 0.03 (0.02,0.05); <0.01 (<0.01,0.07)
elevation + forest structure	-0.05 (0.15); -0.03 (0.11)	846.19	-	-	-	0.02 (-0.01,0.06)	1.39 (1.21,1.57)	0.21 (0.14,0.28); 0.08 (0.04,0.08)
elevation + disturbance	-0.03 (0.16); 0.03 (0.11)	856.49	-	<0.001 (~0)	-	0.08 (0.04,0.12)	1.28 (1.1,1.5)	0.24 (0.17,0.32); 0.05 (0.01,0.08)
elevation	-0.04 (0.16)	860.89	-	-	-	0.10 (0.06,0.14)	1.35 (1.2,1.5)	0.244 (0.17,0.32)
elevation	-0.04 (0.16)	863.32	-	<0.001 (-0.03,0.03)	-	-	1.35 (1.2,1.5)	0.244 (0.17,0.31)
lemur food tree abundance	0.09 (0.09)	929.56	-	0.25 (0.17,0.32)	-	0.08 (0.04,0.07)	1.44 (1.3,1.6)	0.05 (0.02,0.09)

Figure 6.1.
Graphical representation of the hypothesized relationships between abiotic and biotic environmental variables and lemur community structure, as investigated in this study. A) The regional species source pool is the total set of species that could potentially occur in local communities. Environmental filtering and limiting similarity are the main processes of local community assembly. In local communities, tips with dots represent species present in the local community, and dot size represents abundance. Communities are phylogenetic clustering when closely related species co-occur, while communities are overdispersion when distantly related species co-occur. Either pattern can occur under the two assembly processes, depending on the distribution of adaptive traits. When close relatives share traits from common ancestry, phylogenetic clustering is predicted under environmental filtering, and overdispersion is predicted under limiting similarity. In contrast, close relatives may co-occur when they diverge in traits (character displacement), while distant relatives may co-occur under environmental filtering when they converge on adaptive traits. B) The predicted relationships between environmental factors and phylogenetic community composition in this study.

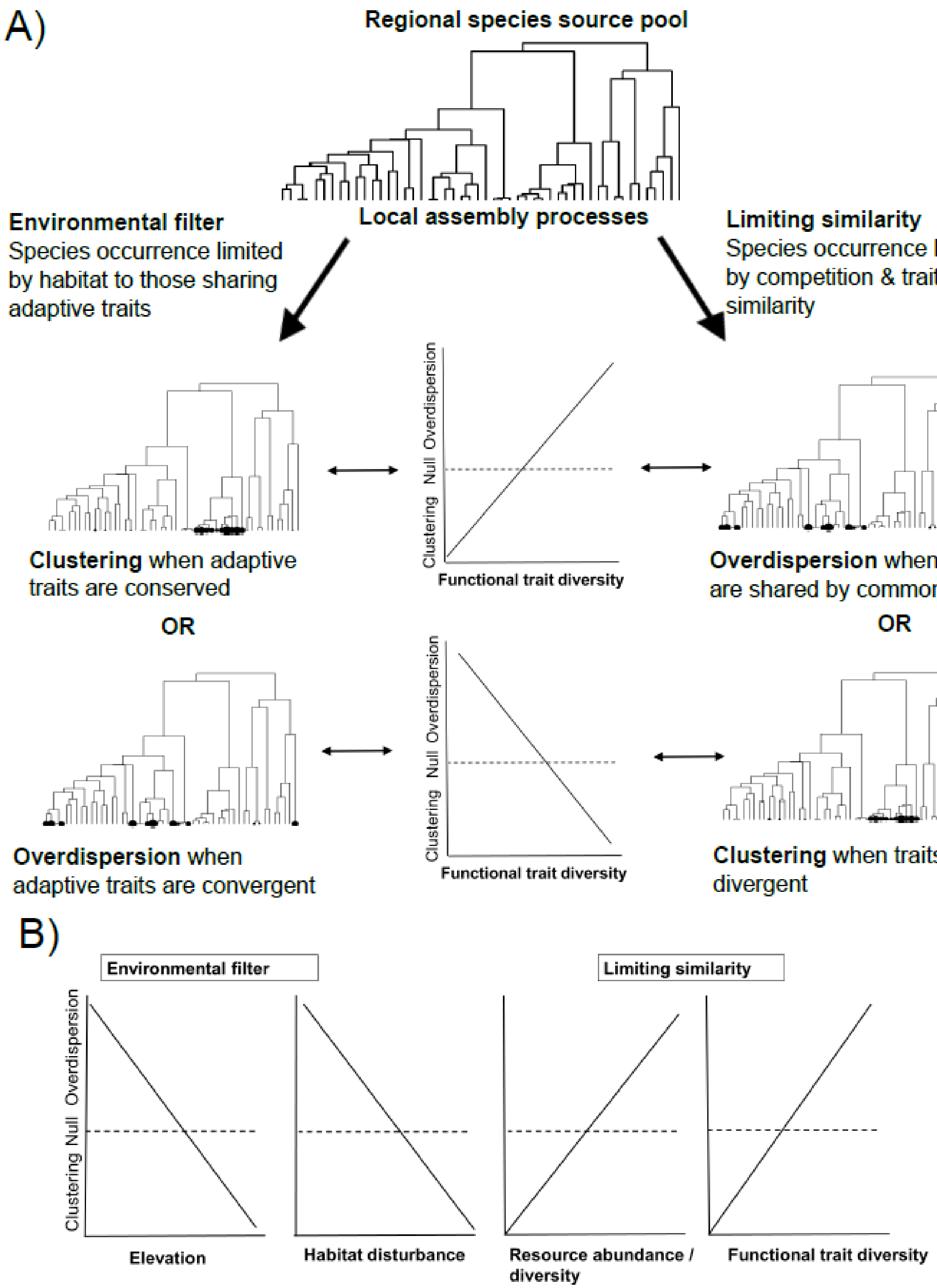
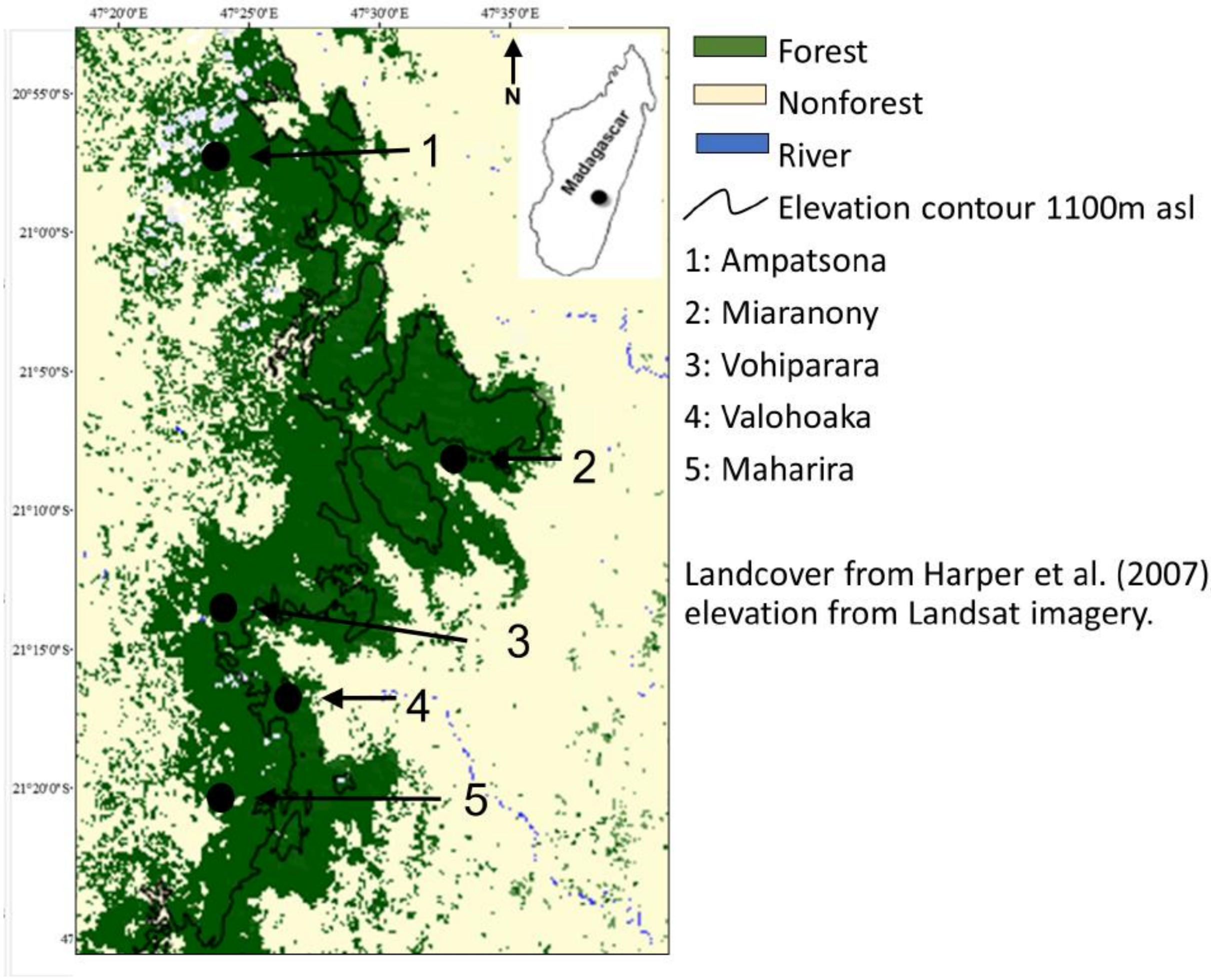

A)
Regional species source pool
Local assembly processes
Environmental filter
Species occurrence limited by habitat to those sharing adaptive traits
Limiting similarity
Species occurrence limited by competition & trait similarity
Clustering when adaptive traits are conserved
Overdispersion when traits are shared by common
OR
OR
Overdispersion when adaptive traits are convergent
Clustering when traits are divergent
Clustering Null Overdispersion
Functional trait diversity
Clustering Null Overdispersion
Functional trait diversity
B)
Environmental filter
Limiting similarity
Clustering Null Overdispersion
Elevation
Habitat disturbance
Resource abundance / diversity
Functional trait diversity

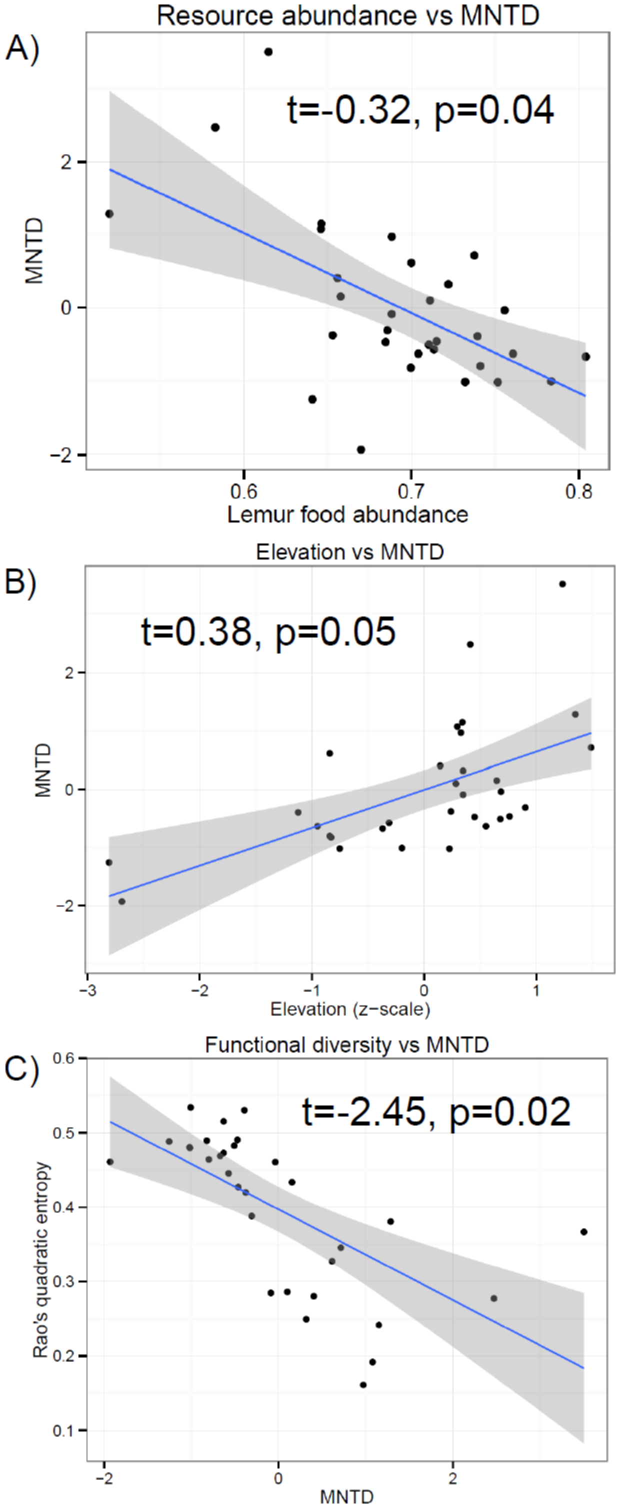
Figure 6.2.

Map of localities surveyed for lemur abundance, botanical composition and structure, elevation and anthropogenic disturbance. Surveys were conducted in contiguous forest at five localities in southeast Madagascar, including one in the Ambositra-Vondrozo corridor (also known as the CoFAV, Schwitzer et al. 2013, locality # 1) and four in Ranomafana National Park (RNP , localities #2-5). The forest cover is depicted in green from Landsat imagery classified by Harper et al. (2007) and an elevation contour line is drawn at 1100m above sea level to illustrate the approximate transition from mid-elevation rainforest on eastern slopes to high-elevation subhumid forest on the western plateau.



Landcover from Harper et al. (2007), elevation from Landsat imagery.

Figure 6.3.
Relationship between phylogenetic community structure (abundance weighted mean nearest taxon distance), environmental variables, and functional trait diversity. The effects of the proportion of food trees on transects (A), elevation (B), and functional trait diversity (C) are shown. The statistics reported are the results from linear mixed model analyses.



CHAPTER SEVEN

CONCLUSION

Biodiversity and evolutionary processes

In this dissertation, I tested the relative roles of abiotic and biotic evolutionary mechanisms generating biodiversity. I compared evolutionary and ecological dynamics from small to large geographic scales. At the broadest geographic scales, speciation, extinction, and dispersal should affect diversity, while at local community scales, interspecies competition for limiting resources should affect species richness and abundance (Cavender-Bares et al. 2009; Kraft and Ackerly 2010; Ricklefs 1987; Swenson et al. 2006). These processes are predicted to leave detectable signals in the phylogeny, geographic distributions, phenotypes and niches of species.

The signals of macroevolutionary processes that are predicted in phylogenies and phenotypes vary with geographic scale. At broad scales, ecological processes related to the theory of adaptive radiation cause higher speciation and phenotypic evolutionary rates in lineages that have access to open niches, while lineages that do not have that access have lower speciation and phenotypic diversity (Schluter 2000b). At regional scales, vicariance causes descendant lineages to inherit unique parts of a widespread ancestral geographic range, while founder effect speciation causes descendant lineages to inherit new ranges outside of the ancestral distribution (Matzke 2013; Ronquist 1997). At local community scales, environmental filters cause species with adaptive traits to co-occur. If species share traits from common ancestry, then close relatives will co-occur more often than distantly related species while if traits are convergent, then distant relatives will co-occur more often than close relatives (Cavender-Bares et al. 2009; Kraft and Ackerly 2010). These predicted outcomes of evolutionary processes can help tease apart their relative roles in generating biodiversity.

I focused on one group of primates, the Strepsirrhini, especially the Lemuriformes. I examined three broad interrelated evolutionary mechanisms: adaptive radiation, biogeography, and interspecies competition. First, lemurs have been posited to have evolved via an adaptive radiation (Martin 1972). To test this hypothesis, I compared the speciation and phenotypic evolutionary rates of lemurs, which had the ecological opportunity of colonizing Madagascar, to their African and Asian sister clade, the Lorisiformes. Second, within Madagascar, abiotic and biotic factors have been suggested to shape the distribution of species, leading to regions of high microendemism (Ganzhorn et al. 2006; Martin 2000; Wilmé et al. 2006). I tested biogeographic hypotheses to infer deep and recent causes of change in regional diversity. Third and most locally, species distributions and abundances should be predicted by interspecies competition for limited resources (Cavender-Bares et al. 2009; Kraft and Ackerly 2010). I compared the population densities of co-occurring species, their phylogenetic relatedness and their functional traits among local communities that varied in habitat characteristics, especially resource abundance. By examining lemur evolution at these different scales, I compared the strength of support for different mechanisms driving species diversity.

Phylogenetic systematics

In this dissertation, I investigated evolutionary mechanisms that may have led to the diversity of lemurs. Lemurs are species rich, with over 100 extant species and at least 17 giant species that went extinct within the last 2000 years (Godfrey et al. 2010; Schwitzer et al. 2013). They are a monophyletic group, indicating a single origin followed by isolated evolution (Yoder and Nowak 2006). Macro-level ecological and evolutionary predictions can be tested a phylogenetic framework (Felsenstein 1985; Nunn 2011). The geographic distributions of species, their functional traits, and their evolutionary relationships elucidate the mechanisms driving speciation. Patterns of species divergence times are indicative of speciation rates (Pybus and Harvey 2000), the timing of events in relation to geological phenomena (Hoorn et al. 2010), and the amount of time for traits to evolve (Klaczko et al. 2015), species to co-exist (Rabosky and Glor 2010), and co-evolutionary forces to operate (Morran et al. 2011). Therefore, a robust estimate of the phylogeny and divergence times of study species is fundamental to understanding their evolution. Improvements in molecular techniques and the public availability of DNA sequences has led to the sequencing of genes for nearly all lemurs, yet no study has attempted to infer a complete phylogeny. The relationships among clades has been difficult to infer, however, because of the rapid divergence of lineages early in their radiation (Horvath and Willard 2007). Further, divergence times have not been calibrated *within* lemurs because there is no true fossil record. Lastly, great progress has been made to place the extinct giant lemurs in the tree with both morphological and molecular data (Jungers et al. 1991; Karanth et al. 2005; Kistler et al. 2015; Orlando et al. 2008). These advances and limitations on our current understanding of lemur phylogenetic systematics led me to use a combined analysis of morphology and molecules for nearly all lemurs.

To test hypotheses of evolutionary mechanisms driving the diversification of lemurs, I first inferred a near-complete phylogeny (88% of lemurs) and estimated divergence times based on 33 fossils in the tree (Heath et al. 2014; Ronquist et al. 2012). I used a total evidence approach (Ronquist et al. 2012), combining morphological and genetic data, to integrate the topological and temporal information captured with fossils (369-421 dental, cranial, postcranial and soft tissue characters, six molecular loci, 5767 bases). I dated trees using the latest techniques to incorporate the temporal and phylogenetic information contained in fossils, with 13 subfossil lemur and 20 fossil primate species. I found strong support for the topological relationships among lemurs including the extinct species. The new dating techniques integrating fossil tips in the tree results in divergence times that are more recent than dates inferred from molecular data. Specifically, I estimated the divergence of haplorhine and strepsirrhine primates to be ~60 million years ago (Ma), rather than 65+Ma as previously hypothesized (Perelman et al. 2011; Springer et al. 2012). Given that the first true fossil primates are from the earliest Eocene, the pre-Cretaceous molecular divergence times were most likely over-estimates (Steiper and Seiffert 2012). The new dating techniques I used capture more information from the fossil record than previous node-calibration methods, and for organisms with a good fossil record, this may dramatically improve the accuracy of divergence-time estimates (Grimm et al. 2014; Heath et al. 2014). I estimated that lemurs originated ~50 Ma, and subsequent divergences of major lineages (taxonomic families) occurred during the end-Eocene, throughout the Oligocene and Miocene. The relationships among most lineages were well resolved, including for extinct taxa, while recent clades with high species richness and short internodes were poorly resolved (e.g., *Microcebus*). Most importantly, by including nearly all lemurs, the phylogenies I inferred provide a robust framework for my comparative analyses of evolutionary mechanisms. These results have important implications for the diversification dynamics that led to disparities in diversity across the primate tree.

Adaptive radiation

Madagascar has been an isolated island since 80-90 Ma, and there is no Tertiary fossil record. The five extant (plus two extinct) mammalian clades are inferred to have arrived via dispersal because their molecular ages post-date the break-up of the Gondwanan landmasses. Lemurs most likely arrived shortly after the origins of true primates 50-60 Ma, with no mammalian or avian competitors or predators that we know of until relatively recently, 5-30 Ma, except for the elephant bird which may have been on Madagascar since the Cretaceous (Yoder and Nowak 2006). Lemurs diversified to fill myriad niches in climates ranging from tropical rainforests to deserts. The species richness and natural history of lemurs led to early hypotheses for the mechanisms generating such diversity.

The predominant view of lemur diversification posits they evolved via an adaptive radiation (Martin 1972). Lemurs had an ecological opportunity to diversify rapidly when they colonized Madagascar that was unavailable to their mainland relatives. Based on the ecological theory of adaptive radiation (Schluter 2000b), lemurs are predicted to have had high speciation and phenotypic evolutionary rates early in their evolution, and these rates should have been higher than those of mainland strepsirrhines, the lorisiforms. Further, early rapid phenotypic diversification should have been related to shifts in niches and occupying unique adaptive zones.

I tested these hypotheses by estimating the rates of lineage and phenotypic diversification rates from the strepsirrhine phylogeny and testing for a shift in the rates across the tree. My results partially support the adaptive radiation hypothesis. Lemur speciation rates increased rapidly after colonizing Madagascar, and continued to rise until recently. Lemur body mass evolved most rapidly after colonization and the evolutionary rate decreased towards the present. In contrast, lorisiforms had gradual rates of speciation and phenotypic evolution. There was a significant shift in phenotypic evolutionary rates after the divergence of *Daubentonia* from other lemurs. One of the predictions of the adaptive radiation theory was not met; no distinct shift in lineage diversification rate was apparent between lemurs and lorisiforms. Body mass evolved towards unique body mass optima and at different rates related to adaptive zones of dietary and activity pattern niches. The lemurs and lorisiforms offered a unique test of the ecological theory of adaptive radiation.

The observation that lemur speciation rates did not decline in diversification rates suggests that lemur diversity was not limited by competition or resource availability, as predicted from the ecological limits hypothesis (Rabosky 2009; Rabosky and Hurlbert 2015). What drove increasing speciation rates through time? Possible explanations include Red Queen effects (Van Valen 1976) such as the arrival of carnivores ~ 30 Ma after lemurs had been diversifying (Yoder and Nowak 2006), and the coevolution of lemurs and their plant resources and/or parasitic enemies (Ricklefs 2010). Biogeographic factors could also explain increasing speciation rates through time, as shifts in climate and habitat, vicissitudes of dispersal barriers and ecological adaptation would result in perpetually changing ecological opportunities (Fritz et al. 2012). These diverse ecological hypotheses of diversification dynamics can be tested in unique ways with the lemurs as a model system.

Historical and ecological biogeography

Lemurs are distributed in rainforest, dry deciduous forests, and spiny deserts. The phylogeography of several clades led to the hypothesis that species evolved via ecological speciation into different habitat niches followed by vicariance due to riverine dispersal barriers (Martin 2000). Alternatively, microendemism may have resulted from recent vicariance events related to Pleistocene climate oscillations (Wilmé et al. 2006). These alternate hypotheses should leave distinguishable signals on the phylogenetic relatedness of species and communities (Graham et al. 2014; Graham and Fine 2008).

Based on predictions from macroevolutionary theories, if abiotic factors split ancestral ranges and phylogenetic niche conservatism led to descendants maintaining ancestral niches (Wiens and Graham 2005), then geographic distance should be a strong predictor of phylogenetic structure but not trait differences (Graham et al. 2014). With vicariant speciation, there is no expected relationship between phylogeny, functional traits and environmental variables because abiotic factors caused population fragmentation as individuals tracked ancestral niches (phylogenetic niche conservatism, Wiens et al. 2010; Wiens and Graham 2005). If environmental adaptations drive speciation, then ecological factors should be strong predictors of phylogenetic structure and ecologically relevant traits should be divergent in different habitats (Graham and Fine 2008; Graham et al. 2009). If interspecies interactions drive species distributions, especially competition, then niche partitioning should be evident in phylogenetic and functional trait divergence (Webb et al. 2002). Widespread ecological adaptation should result in coincident species distributions across lineages in relation to environmental gradients such that the taxonomic, phylogenetic and functional similarity of whole communities is predicted by environment (Graham and Fine 2008). In contrast, repeated vicariant speciation in lowland regions should result in closely related species co-occurring less frequently because populations are separated by dispersal barriers (Vamosi et al. 2009).

I compared the roles of climate, habitat, geographic dispersal barriers, and interspecies competition in shaping lemur biogeography. I compared the geographic hypotheses of vicariance and dispersal using a likelihood approach explicitly designed for historical biogeography (Matzke 2014). I found that a combination of biogeographic events, especially founder-event speciation, vicariance, and within-region diversification explain the geographic distribution of species. Widespread ancestors were common, and subsequent microendemic lineages most likely evolved from descendant lineages inheriting a single portion of the range (akin to parapatric speciation or peripheral budding), and vicariance. Dispersal was common, especially to and from the central highlands and between the northwest and northeast, supporting the hypothesis of a north/south dispersal barrier and east/west connectivity (Ganzhorn et al. 2006; Yoder and

Heckman 2006). Temporal changes in dispersal probabilities related to previously hypothesized barriers to dispersal were not supported; instead, geographic distance alone was a significant predictor of lemur phylogenetic diversity and distribution.

I quantified the taxonomic, phylogenetic, and functional alpha and beta composition of 50 modern and five subfossil lemur communities from island-wide to local scales. The best predictor of the phylogenetic similarity of sites was plant productivity, suggesting that the most important factor driving geographic structure in community similarity is related to resource availability. There was clear geographic structure in the phylogenetic similarity of communities corresponding to bioregions of the island subdivided by river barriers. After controlling for the effects of plant productivity on the phylogenetic similarity of communities, there was a negative relationship between phylogenetic similarity and distance; geographically close communities were more dissimilar phylogenetically than expected from the taxonomic diversity, indicating near-by localities consist of paleoendemics (Graham and Fine 2008).

Within pre-extinction Holocene communities (alpha diversity), the phylogenetic relatedness of co-occurring species was not different from null expectations and trait diversity was high across all regions. In post-extinction modern communities, species in the northwestern region were more closely related than expected from the null community and had lower trait diversity, while the central highlands consisted of distantly related species. These differences in regional alpha diversity suggest that recent extinction significantly changed the regional species pools, counter to the results of a recent study (Razafindratsima et al. 2013). In modern local communities within regions, co-occurring species were more distantly related than expected from a randomly-assembled community and trait diversity was high, suggesting that niche-partitioning shapes community composition. The positive relationship between species richness, functional trait diversity and phylogenetic diversity suggests that niche diversity is greatest when species are most distantly related. Diversity was highest in communities with the highest plant productivity, especially in the dry season, suggesting that low dry-season productivity limited the diversity of western and southern forests. These results support earlier hypotheses for the biogeographic evolution of lemurs. Specifically, higher diversity in eastern than western forests, positively related to plant productivity supports hypotheses emphasizing the specific roles of botanical variables on lemur community ecology (Ganzhorn et al. 1997; Ganzhorn et al. 1999). The results highlight the importance of including extinct subfossil lemur communities in biogeographic inference because these phylogenetically and functionally diverse communities were found in the west and central highlands, where modern lemur communities now have lower diversity.

Local community ecology, environmental filtering, and interspecies competition

While broad-scale differences in environmental regimes and geographic dispersal barriers explain lemur community composition across the entire island, local community assembly within a single regional species pool should be driven by interspecific competition (Cavender-Bares et al. 2009, Swenson et al. 2007, Kraft et al. 2010). Earlier studies of niche partitioning among sympatric lemurs suggested that competition was avoided by parsing the environment along temporal, spatial, and dietary axes (Ganzhorn 1997; Ganzhorn 1988; Ganzhorn 1992; Ganzhorn 1995; Wright 1999; Wright and Jernvall 1999; Wright et al. 2011). I tested the hypothesis that competition is the predominant process shaping local community assembly.

I compared the relative abundances of species among transects distributed along gradients of elevation, human disturbance, structural complexity and resource availability. I quantified lemur abundance as well as the abundance of their preferred food trees on 31 transects within a single region, southeast Madagascar. At this geographic scale, processes such as *in situ* speciation and dispersal barriers should be limited and heterogeneity in resource abundance should be the predominant limitation to lemur diversity through density-dependent effects (the “Darwin-Hutchinson zone”, Vamosi et al. 2009). The functional diversity of communities was quantified based on trait dissimilarity related to body size, diet, life history, and sociality.

I found that the strongest predictors of lemur diversity were resource abundance and elevation. In contrast to the pattern of phylogenetic overdispersion observed at island-wide and regional scales, lemur communities at local scales ranged from overdispersed at high elevations and where resources were limited, to phylogenetically clustered where resources were abundant. Where resources were most abundant, lemur communities were composed of closely related species that were ecologically dominant (i.e., had high relative abundance). Where resources were scarce, such as at high elevations, communities were composed of distantly related species. Functional diversity was highest where communities were clustered and lowest where communities were overdispersed. This result can be explained by the relative paucity of large-bodied frugivorous species and predominance of small nocturnal folivores in overdispersed communities. There is strong evidence that closely related species and those with similar body mass tend not to co-occur, supporting a role of character displacement in structuring community assembly (Schluter 2000a). Further, species-specific responses to elevation explain the most variance in species’ relative abundances, and close relatives have opposite responses to elevation. For example, *Eulemur rufifrons* has a negative response to elevation while its congener *E. rubriventer* has a positive response, suggesting an evolutionarily inherited habitat partitioning along the elevation gradient.

These results corroborate earlier hypotheses that tree community composition, especially food tree relative abundance, is a significant predictor of lemur community dynamics through clade-wide (Ganzhorn et al. 1997) and species-specific effects (Arrigo-Nelson 2006; Balko and Underwood 2005; Irwin 2008; Sterling 1994). There is strong support for coevolutionary relationships between lemurs and plants, which has been suggested based on the apparent niche partitioning in preferred food tree species among frugivores (Wright et al. 2011) and the role of lemurs as seed dispersers (Razafindratsima et al. 2014).

What do lemur evolutionary dynamics tell us about ecological limits?

A recent paradigm in macroevolutionary studies, the ecological limits hypothesis, predicts that diversification rates (speciation minus extinction) are diversity-dependent. That is, as species richness increases over time, diversification rates decrease because diversity has a carrying capacity set by resource limitation (Rabosky and Hurlbert 2015). The following observations have led to growing support for the ecological limits hypothesis: the prevalence of slow-downs in diversification rates through time, the lack of relationship between clade age and species richness, the positive relationship between species richness, area and habitat productivity, and the apparent constancy of species richness in the paleontological record. These same patterns can be explained by mechanisms that do not assume a carrying capacity (Harmon and Harrison 2015). Slow-downs in diversification rate are often confounded by statistical artifacts of incomplete sampling and phylogenetic model misspecification. Further, the classic “early burst” of lineage and phenotypic evolution is uncommon in comparative analyses (Harmon et al. 2010), and with ancient radiations, the early burst pattern may have eroded over time. No relationship between clade age and species richness indicates that older clades are not more species rich than younger clades, suggesting some limitations to speciation rate obscure the expected pattern. The lack of a pattern is not strong evidence of a process, and many processes may influence such a statistical test. High habitat productivity may be related to species richness because clades originated in high productivity areas (e.g., the tropics) and have maintained the same range, giving them more time for speciation (Wiens et al. 2006). Lastly, the paleontological record shows clear instances of changes in diversity over time (Huang et al. 2015), and rather than assume a constantly changing equilibrium, it is more likely that there is no observable equilibrium, or if there is one species are not reaching it at large geographic scales (Harmon and Harrison 2015).

Lemur evolutionary history shows mixed support for the ecological limits hypothesis. First, diversification rates did not decline over time; rather, they increased throughout the lemur tree over time. The ecological limits hypothesis predicts that lemurs should have reached an equilibrium, given the amount of time lemurs have been evolving on Madagascar and the fact that niche variables related to body mass, diet and activity appear to have evolved early and remained stable. Increasing speciation rates through time is not concordant with an ecological limit to diversity. Instead, it suggests that many factors have acted during the long geological history of evolution, including biogeographic range shifts.

Lemur biogeography suggests that regions are not saturated with species because multiple dispersal events, including founder event speciation, were inferred to occur. If regions were at equilibrium, dispersal should be limited because regions are packed with species. The ecological community structure strongly supports a positive relationship between habitat productivity and species, phylogenetic, and functional diversity. The phylogenetic aspect of community diversity is informative on the evolutionary time scale separating communities. Phylogenetic beta diversity among high and low productivity sites was higher than expected by taxonomic diversity, indicating long evolutionary time periods separating communities in high and low productivity sites and supporting the time-for-speciation hypothesis rather than the ecological limits hypothesis. Further, the high functional diversity and lack of functional redundancy within communities in high productivity localities suggests communities are not saturated, as would be expected if they had reached ecological limits (Petchey and Gaston 2002).

Lastly, at the most local scales, if resources were limiting, then low resource sites should have the lowest species richness and phylogenetic diversity, while high resource abundance is predicted to have the highest species richness and phylogenetic diversity. I found that local communities of lemurs exhibited the opposite pattern. Communities with the most abundant resources were dominated by a few closely related species which diverged in traits, while low resource communities were more taxonomically and phylogenetically even and had low trait diversity. These results show that the processes governing community assembly are not as simple as a positive relationship between resources and diversity. Further, scale is an important factor in the ecological limits hypothesis. At all scales, the ecological limits hypothesis predicts a negative relationship between species richness and diversification because of competition for limiting resources. At the island-wide scale, however, not all lemurs are actually or potentially interacting. The biogeographic results clearly show that species richness was divided among multiple areas such that only a subset of species would potentially compete at any time, and even those species that co-occur partition the habitat along fine niche axes to maximize resource use (Ganzhorn 1988). The results of this dissertation studying lemur evolution do not support the ecological limits hypothesis, and show that factors affecting diversity are scale and time dependent.

In summary, my dissertation research has approached primate evolution and biogeography from phylogenetic and ecological perspectives to gain a holistic picture of the mechanisms driving diversity. Increasing speciation rates through time may have been maintained by biotic factors such as the late arrival of predators and competitors. Ecological adaptation and geographic separation clearly shaped lemur diversity and distributions in deep time. Local community assembly was related to plant productivity, resource abundance, and the ability of some species to attain ecological dominance. The results highlight that environmental and geographic variables operating at different scales affected the evolution of lemur diversity leading to disequilibrium dynamics. This study also highlighted the recent anthropogenic changes that perturbed diversity patterns. In this dissertation, for the first time, the evolutionary history of lemurs was explained in a comprehensive phylogenetic, biogeographic, and ecological framework leading to new insights on the mechanisms of lemur diversification.

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APPENDIX I

Supplemental information included with Chapter Two, Combined analysis of living and fossil species.

Supplemental Information 1. Character and state descriptions for 421 morphological characters indicating the partition (cranial, mandibular, dental, postcranial, soft tissue, physiological). Characters that were omitted based on 0 Gower dissimilarity are shaded in grey. For dental characters, lower case letters denote the mandibular teeth (e.g., m1 = lower first molar) and upper case denotes the maxillary teeth (e.g., M1 = upper first molar). Polymorphisms are coded as an intermediate state (e.g., state 1 is coded ‘0/2’, meaning individuals of a species have state 0 or state 2).

1. lower incisor # (Ross et al. 1998 character i1)
    0 three in each quadrant
    1 two in each quadrant
    2 one in each quadrant
    3 no incisors

2. lower incisor occlusal arrangement (Ross et al. 1998 character i2)
    0 arcuate battery "U"
    1 cusp tips staggered "V"

3. lower incisor crown height
    0 low
    1 0/2
    2 moderate
    3 2/4
    4 high

4. lower incisor crown orientation
    0 erect or vertical
    1 0/2

- 2 procumbent
- 3 2/4
- 4 very procumbent

5. lower incisor root orientation (Ross et al. 1998 character i11)
    - 0 erect or vertical
    - 1 0/2
    - 2 slightly procumbent
    - 3 2/4
    - 4 very procumbent

6. first lower incisor shape
    - 0 spatulate
    - 1 pointed or lanceolate

7. i1:i2 (Ross et al. 1998 character i6)
    - 0 i1:i2 ratio <0.65
    - 1 0/2
    - 2 ratio=>0.65, <0.82
    - 3 2/4
    - 4 ratio =>0.83, <1
    - 5 4/6
    - 6 ratio =>1.01,<1.25
    - 7 6/8
    - 8 ratio =>1.25

8. i1-2 area relative to m1
    - 0 small (=<0.69)
    - 1 intermediate (=>0.70, =<1.07)
    - 2 large (>0.70)

9. i1 to m1 area (Ross et al. 1998 character i19)
    - 0 i1 area << m1 area
    - 1 0/2
    - 2 i1 area < or = m1 area
    - 3 2/4
    - 4 i1 > m1

10. i1 lingual cingulum
    - 0 absent or weak
    - 1 0/2
    - 2 strong incomplete
    - 3 2/4
    - 4 strong complete

11. i2 cross sectional shape (Ross et al. 1998 character i8)

0 ratio =>0.64
1 <0.64

12. i2 heel development (Ross et al. 1998, character i15)
0 heel absent
1 heel present

13. female canine maximum cross-sectional area relative to first lower molar area (Ross et al. 1998 character c1, modified)
0 c1 area/m1 area < 0.40
1 0/2
2 c1 area/m1 area =>0.4, <0.8
3 2/4
4 c1 area/m1 area =>0.8, <=1.2

14. lower canine cross-sectional shape
0 rounded oval
1 mesiodistally compressed
2 buccolingually compresed

15. canine in toothcomb (modified from Seiffert et al. 2015, which was modified from Ross et al. 1998 character i13)
0 lower canine not incorporated into a toothcomb
1 lower canine incorporated into toothcomb

16. lower canine height
0 low, squat
1 0/2
2 narrow,short
3 tall, at or above toothrow
4 high crowned but very procumbent
5 no lower canine

17. lower canine paracristid
0 oblique to occlusal plane
1 nearly horizontal
2 forms part of a cropping mechanism with i1-2
3 oriented in line with buccal face of adjacent incisor

18. lower canine lingual crest
0 rounded
1 0/2
2 sharp

19. orientation of lower canine root
0 oriented in line with long axis of crown

1 mesially inflected

20. lower premolar crowding (Ross et al. 1998 character p5)
    0 no crowding
    1 0/2
    2 slightly crowded
    3 2/4
    4 very crowded

21. lower premolar inflation (Ross et al. 1998 character p29)
    0 not basally inflated
    1 0/2
    2 slightly basally inflated
    3 2/4
    4 very basally inflated

22. premolar orientation
    0 crown bases vertical
    1 0/2
    2 slightly oblique
    3 2/4
    4 strongly oblique, projecting mesially

23. p1 presence
    0 present
    1 0/2
    2 absent

24. p2 buccal cingulum development
    0 absent
    1 0/2
    2 incomplete, broken at protoconid and hypoconid
    3 2/4
    4 complete

25. p2 metaconid
    0 metaconid absent or indistinct
    1 0/2
    2 metaconid small
    3 2/4
    4 large

26. p2 protoconid height and shape
    0 extremely short, shorter than p3
    1 0/2
    2 not projecting, in line with p3

3 2/4
4 slender, projects above protoconids of p3-4
5 4/6
6 massive projects above protoconids of p3-4

27. p2 roots/presence
0 two
1 0/2
2 one
3 2/4
4 absent

28. p3:p4 area
0 <0.45
1 0/2
2 0.45-0.59
3 2/4
4 0.60-0.69
5 4/6
6 0.70-0.79
7 6/8
8 >0.80

29. p3-4 protoconid height
0 p3 much lower than p4
1 0/2
2 p3 slightly lower than p4
3 2/4
4 p3 equal in height to p4
5 4/6
6 p3 higher than p4

30. p3 entoconid and lingual talonid
0 absent
1 0/2
2 lingual talonid crest present but an entoconid does not stand out above it
3 2/4
4 entoconid is small discrete cusp

31. p3 lateral protocristid orientation
0 transverse
1 0/2
2 distal or distolingual
3 2/4
4 absent

32. p3 lingual cingulum
    0 present
    1 0/2
    2 absent

33. p3 metaconid size
    0 absent
    1 0/2
    2 present small
    3 2/4
    4 present, large

34. p3 paraconid
    0 present, large
    1 0/2
    2 present small
    3 2/4
    4 negligible or absent

35. p3 root orientation (contains information similar to Ross et al. 1998 character p45)
    0 mesial root placed directly mesial to distal root
    1 0/2
    2 mesial root placed lateral to distal root

36. p3 roots
    0 one
    1 0/2
    2 two

37. p4:m1 area
    0 <0.62
    1 0/2
    2 >0.63,<0.72
    3 2/4
    4 >0.73, <0.82
    5 4/6
    6 >0.83,<0.92
    7 6/8
    8 >0.93

38. p4 buccal cingulum
    0 absent or indistinct
    1 0/2
    2 present and distinct

39. p4 cristid obliqua

0 absent
1 0/2
2 weak
3 2/4
4 strong

40. p4 entoconid and lingual talonid
0 absent or trace
1 0/2
2 lingual talonid crest present but entoconid does not stand out above it
3 2/4
4 entoconid is small discrete cusp

41. p4 exodaenodonty (Ross et al. 1998 character p30)
0 not exodaenodont
1 slightly exodaenodont
2 very exodaenodont

42. p4 hypocristid shearing development (Ross et al. 1998 character p27)
0 absent
1 0/2
2 weak
3 2/4
4 strong

43. p4 lateral protocristid morphology (contains information similar to Rp21-42 and Rp23-44)
0 protocristid poorly developed or absent
1 0/2
2 distolingually oriented protocristid present
3 2/4
4 trenchant and tranversely oriented protocristid present

44. height of p4 talonid
0 no aspect of talonid is at level of m1 trigonid
1 0/2
2 hypoconid extends to level of m1 trigonid
3 2/4
4 entire talonid basin extends to level of m1 trigonid

45. p4 lingual cingulum
0 absent or discontinuous
1 0/2
2 present and distinct

46. p4 md length/bl width (Ross et al. 1998 character p43)
0 <0.95

- 1 0/2
- 2 >0.96, <1.14
- 3 2/4
- 4 >1.15, <1.35
- 5 4/6
- 6 >1.36, <1.46
- 7 6/8
- 8 >1.47

47. p4 metaconid
    - 0 absent or indistinct
    - 1 0/2
    - 2 small
    - 3 2/4
    - 4 large

48. p4 metaconid and protoconid space
    - 0 close to protoconid
    - 1 0/2
    - 2 widely spaced from protoconid

49. p4 paraconid
    - 0 p4 paraconid present and large
    - 1 0/2
    - 2 present small
    - 3 2/4
    - 4 very small/absent

50. p4 paraconid position
    - 0 mesial to protoconid
    - 1 mesiolingual, between proto and metaconid
    - 2 mesial to metaconid but widely spaced from it

51. p4 postmetacristid (contains information similar to Ross et al. 1998 character p37)
    - 0 weak or absent
    - 1 0/2
    - 2 moderate
    - 3 2/4
    - 4 very strong

52. p4 postprotocristid (Ross et al. 1998 character p36)
    - 0 weak or absent
    - 1 0/2
    - 2 moderate
    - 3 2/4
    - 4 very strong

53. p4 premetacristid (Ross et al. 1998 character p18, modified)
0 premetacristid absent or poorly developed
1 0/2
2 premetacristid present

54. p4 root number
0 one
1 two

55. length of p4 talonid
0 =>1.27,<1.61
1 0/2
2 =>0.92,<1.27
3 2/4
4 <0.9

56. mesiodistal postion of p4 meta and protoconid
0 metaconid distal to protoconid
1 0/2
2 metaconid is transverse to protoconid

57. position of p4 hypoconid or distal terminus of p4 cristid obliqua
0 buccal to protoconid
1 0/2
2 distal to protoconid
3 2/4
4 between protoconid and metaconid
5 4/6
6 distal to metaconid

58. lower molar metastylids (Ross et al. 1998 character m12)
0 absent
1 0/2
2 trenchant postmetacristid or incipient metastylid
3 2/4
4 present, large

59. m1-2 basal cusp inflation
0 crestiform
1 0/2
2 moderate basal inflation
3 2/4
4 cusp bases bulbous

60. m1-2 buccal cingulum

0 absent to trace
1 0/2
2 partial, discontinuous
3 2/4
4 complete

61. m1-2 hypocristid development (Ross et al. 1998 character m38)
0 absent or indistinct
1 0/2
2 weak
3 2/4
4 strong

62. m1-2 talonid lingual configuration
0 open
1 0/2
2 notched lingually or closed

63. m1 area (Ross et al. 1998 character m54)
0 1.10-3.00 mm
1 0/2
2 3.10-5.00 mm
3 2/4
4 5.10-7.00 mm
5 4/6
6 7.10-9.00 mm
7 6/8
8 >9.10 mm

64. m1 cristid obliqua
0 reaches trigonid wall at point distal to protoconid
1 0/2
2 reaches trigonid wall at point distolingual to protoconid
3 2/4
4 reaches trigonid wall at a point distal to metaconid

65. m1 cristid obliqua development
0 weak (rounded)
1 0/2
2 strong(trenchant)

66. m1 cristid obliqua terminus
0 runs to base of trigonid
1 0/2
2 runs part way up the distal talonid wall
3 2/4

- 4 connects with protoconid tip or protocrstid
- 5 4/6
- 6 connects with metaconid

67. m1 hypoconulid
    - 0 large
    - 1 0/2
    - 2 moderate
    - 3 2/4
    - 4 small
    - 5 4/6
    - 6 absent

68. m1 length/width
    - 0 1.0-1.15
    - 1 0/2
    - 2 1.16-1.22
    - 3 2/4
    - 4 1.23-1.32
    - 5 4/6
    - 6 >1.33

69. m1 metaconid position
    - 0 approximately transverse to protoconid
    - 1 0/2
    - 2 distal to protoconid

70. m1 paraconid
    - 0 absent or crestiform
    - 1 0/2
    - 2 present, small
    - 3 2/4
    - 4 present, large

71. m1 paraconid position
    - 0 mesial to protoconid
    - 1 mesiolingual
    - 2 1/3
    - 3 mesial to metaconid but widely spaced
    - 4 twinned with metaconid

72. m1 parastylid (Ross et al. 1998 character m11)
    - 0 absent
    - 1 0/2
    - 2 present

73. m1 premetacristid (contains information similar to Ross et al. 1998 character m18)

0 premetacristid absent or indistinct
1 0/2
2 premetacristid present

74. m1 trigonid height

0 higher than talonid
1 0/2
2 slightly higher than talonid
3 2/4
4 trig and tal of similar height

75. hypoconulid position on m1 (contains information similar to Ross et al. 1998 character m30)

0 twinned with, or most closely situated next to, entoconid
1 0/2
2 central
3 2/4
4 closer to hypoconid than to entoconid

76. sulcus between metaconid and protoconid on m1-2 (contains information similar to Ross et al. 1998 character m22 and m23)

0 absent
1 0/2
2 present; protocristids poorly developed or absent

77. m2 cristid obliqua development

0 weak(rounded)
1 0/2
2 strong(trenchant)

78. m2 cristid obliqua orientation

0 reaches trigonid wall distal to protoconid
1 0/2
2 reaches trigonid wall distolingual protoconid
3 2/4
4 reaches trigonid distal to metaconid

79. m2 cristid obliqua terminus

0 runs to base of trigonid
1 0/2
2 runs part way up distal trigonid
3 connects to protoconid tip
4 3/5
5 connects with metaconid

80. m2 entoconid relative to hypoconid

0 mesial to hypoconid
1 0/2
2 transverse to hypoconid
3 2/4
4 distal to hypoconid

81. m2 hypoconulid position
0 twinned with or closest to entoconid
1 0/2
2 central
3 2/4
4 closer to hypoconid than to entoconid

82. m2 hypoconulid size
0 large
1 0/2
2 moderate
3 2/4
4 small
5 4/6
6 absent

83. m2 length/m3 length
0 m3 much longer than m2 (0.71-0.8)
1 0/2
2 m3 longer than m2 (0.81-0.9)
3 2/4
4 slightly longer or equal to m2 (0.91-1)
5 4/6
6 m3 slightly shorter than m2 (1.01-1.12)
7 6/8
8 m3 much shorter than m2 (=>1.13) or absent

84. m2 paraconid
0 absent
1 0/2
2 present, small
3 2/4
4 present, large

85. m2 paraconid position
0 mesial to protoconid
1 0/2
2 equidistance between proto and metaconid
3 2/4
4 mesial to metaconid but widely spaced

5 twinned with metaconid

86. m2 trigonid width (ratio of buccolingual breadths of trigonid and talonid) (Ross et al. 1998 character m6)
0 much wider than talonid (=>1.11)
1 0/2
2 width similar (<1.11,>0.90)
3 2/4
4 much narrower than talonid (=<0.90)

87. morphology of distolingual aspect of m2 (contains information similar to Ross et al. 1998 characters m26 and m41)
0 no postentoconid sulcus
1 hypoconulid closely situated next to entoconid and postentoconid sulcus present, entoconid confluent with distal talonid wall
2 distolingual fovea present, entoconid confluent with posterior talonid wall
3 distolingual fovea present, entoconid mesiodistally abbreviated and not confluent with posterior talonid wall

88. accessory cusps on distolingual aspect of m2
0 absent
1 variably present

89. m3 cristid obliqua terminus
0 absent or indistinct
1 runs to base of trigonid
2 runs part way up distal trigonid wall
3 connects with protoconid tip
4 connects with metaconid

90. m3 entoconid
0 present and distinct
1 0/2
2 greatly reduced or absent

91. m3 hypoconulid
0 lobate
1 0/2
2 not lobate

92. m3 paraconid position
0 mesial to protoconid
1 0/2
2 mesiolingual, between proto and meta
3 2/4
4 mesial to metaconid but widely spaced from it

    - 5 4/6
    - 6 twinned with metaconid

93. m3 paraconid size
    - 0 absent
    - 1 0/2
    - 2 present, small
    - 3 2/4
    - 4 present large

94. m3 root number
    - 0 one
    - 1 two

95. m3 trigonid width (based on relative buccolingual breadths) (Ross et al. 1998 character m7)
    - 0 =>1.20
    - 1 0/2
    - 2 <1.20->1.05
    - 3 2/4
    - 4 <1.05

96. position of m3 hypoconulid
    - 0 centrally located
    - 1 twinned with or next to entoconid
    - 2 bucally located closer to hypoconid

97. molar centroconids (contains information similar to Ross et al. 1998 character m37)
    - 0 absent
    - 1 present

98. molar enamel crenulation
    - 0 smooth
    - 1 0/2
    - 2 slightly crenulated
    - 3 2/4
    - 4 highly crenulated

99. interincisal diastema
    - 0 very broad
    - 1 narrow

100. upper incisor #
    - 0 three
    - 1 two
    - 2 one
    - 3 zero

101. I1:I2
- 0 areas approximately equal or I1 smaller than I2
- 1 0/2
- 2 I1 slightly arger than I2
- 3 2/4
- 4 I1 much larer than I2

102. I1:M1
- 0 small (<0.5)
- 1 moderate (0.5-.56)
- 2 large (>0.56)

103. I1 basal lingual cusp (RI12-125)
- 0 absent
- 1 present

104. I1 crown shape
- 0 spatulate
- 1 0/2
- 2 semispatulate
- 3 2/4
- 4 central occlusal cusp pointed, occlusal edges steep

105. I1-I2 buccal cingulum (RI13-126)
- 0 absent
- 1 present

106. I1I2 interincisal contact
- 0 absent, teeth widely spaced
- 1 0/2
- 2 present as a narrow contact
- 3 2/4
- 4 tightly packed against I1

107. I1 occlusal edge orientation
- 0 occlusal edge approximately orthoganol to long axis of root
- 1 occlusal edge wears at a steep angle to long axis of root
- 2 crown with pronounced mesial asymmetry

108. I1 occlusal shape (mesiodistal length/buccolingual breadth) (RI6-119)
- 0 rounded_oval_(<1.05)
- 1 0/2
- 2 buccolingually_compressed_(>1.05,_<1.30)
- 3 2/4
- 4 extremely compressed_(>1.30)

109. I2-C diastema
    0 present
    1 0/2
    2 absent

110. I2 occlusal shape (mesiodistal length/buccolingual breadth) (RI7-120)
    0 rounded oval (=<1.05)
    1 0/2
    2 slightly buccolingually compressed (>1.05, <1.30)
    3 2/4
    4 extremely_buccolingually_compressed_(=>1.30)

111. C1 lingual cingulum (RC4-130)
    0 weak or absent
    1 0/2
    2 strong
    3 2/4
    4 very strong

112. C1 mesial groove (females) (RC3-129)
    0 shallow or absent
    1 deep

113. upper canine occlusion (RC2-128)
    0 wears_against_p1-2
    1 0/2
    2 wears against p2
    3 2/4
    4 wears_against_p2-3
    5 4/6
    6 wears against p3

114. rotation of upper canine
    0 long axis oriented in line with premolar
    1 slightly rotated internally
    2 strongly rotated internally
    3 absent

115. upper canine shape (contains information similar to RC1-127)
    0 round in cross-section
    1 0/2
    2 oval
    3 2/4
    4 strongly compressed buccolingually

116. canine dimorphism (square root of male lower canine area / square root of female lower canine area)
0 <1.07
1 >=1.07, < 1.17
2 >=1.17

117. P1 presence
0 present
1 absent

118. height of P2 relative to P3
0 smaller than or subequal in height
1 0/2
2 P2 slightly taller than P3
3 2/4
4 P2 much taller than P3

119. P2:P3 area
0 much smaller than P3 (<=0.85)
1 0/2
2 app. same size, or slightly smaller than P3
3 2/4
4 larger than P3

120. P2 occlusal outline (RP6-136)
0 triangular
1 suboval with the long axis buccolingual
2 suboval with the long axis mesiodistal
3 round

121. P2 protocone (RP12-142, modified)
0 present
1 absent

122. P2 root #/presence
0 three
1 two
2 one
3 P2 absent

123. P3-4 buccal cingulum
0 absent or weak
1 0/2
2 strong

124. P3 distal crown margin

0 smoothly rounded
1 0/2
2 waisted between buccal and lingual cusps

125. P3 metacone
0 absent
1 0/2
2 present

126. P3 hypocone
0 absent
1 0/2
2 present

127. P3 protocone
0 absent
1 0/2
2 present small
3 2/4
4 present distinct

128. P3-4 trigon/talon proportions (RP8-138)
0 trigon>=talon
1 trigon<talon

129. P3 root number
0 one
1 0/2
2 two
3 2/4
4 three
5 absent

130. P4 area:M1 area
0 P4<<M1 (<=0.66)
1 0/2
2 P4<M1 (0.66-0.76)
3 2/4
4 P4=M1
5 4/6
6 P4>M1

131. P4 lingual cingulum
0 absent
1 0/2
2 present

132. P4 hypocone
  0 absent
  1 0/2
  2 present

133. P4 metacone
  0 absent
  1 0/2
  2 present

134. P4 metaconules
  0 absent
  1 0/2
  2 present

135. P4 occlusal outline
  0 triangular
  1 suboval
  2 1/3
  3 squared

136. P4 pericone
  0 absent
  1 present

137. P4 postprotocrista
  0 absent
  1 0/2
  2 weak, short
  3 2/4
  4 strong
  5 4/6
  6 strong, secondary postprotocrista directed towards metacone

138. P4 protocone
  0 low relative to paracone
  1 high rel to paracone
  2 absent

139. P4 root number (RP3-133)
  0 one
  1 two
  2 three

140. P4 styles

0 absent
1 parastyles present
2 metastyles present
3 both present

141. upper premolar paraconules (contains information similar to RP14-144)
0 absent or indistinct
1 transverse crest connecting protocone to paracone
2 present

142. M1:M2
0 M1>M2_(<1.40,>1.0)
1 0/2
2 M1=<M2_(=<1.0)

143. M1-2 buccal cingulum
0 absent
1 0/2
2 present poorly developed
3 2/4
4 present, distinct
5 4/6
6 extensive buccal shelf

144. M1-2 hypocone
0 large
1 0/2
2 small
3 2/4
4 absent

145. M1-2 hypocone position (RM12-162)
0 distal, slightly lingual to protocone
1 0/2
2 distal,_far_lingual_to_protocone

146. M1-2 lateral posterior transverse crista development (RM19-169)
0 sharp
1 0/2
2 indistinct

147. M1-2 metaconule size
0 absent
1 0/2
2 small
3 2/4

  4 large

148. M1-2 Nannopithex fold (RM5-156)
  0 absent
  1 0/2
  2 weak
  3 2/4
  4 strong

149. M1-2 paraconule
  0 absent
  1 0/2
  2 small, moderate
  3 2/4
  4 large, as large as protocone

150. M1-2 paraconule position (RM15-165)
  0 attached to preprotocrista
  1 0/2
  2 not attached to preprotocrista

151. M1-2 pericone
  0 absent
  1 0/1
  2 present

152. M1-2 postmetaconule cristae (RM28-174)*
  0 absent or weak
  1 0/2
  2 strong

153. M1-2 postprotocrista
  0 strong runs to base of metaconule or metacone
  1 0/2
  2 strong but short
  3 2/4
  4 absent

154. M1-2 premetaconule cristae (RM27-173)
  0 absent or weak
  1 strong

155. M1-2 root number (RM1-152)
  0 three_or_more,_three_or_more
  1 three,_two

156. M1-2 styles
    0 absent
    1 parastyles present
    2 metastyles present
    3 both present

157. M1-3 anterior cingulum
    0 strong, compelte, long
    1 0/2
    2 strong, short
    3 2/4
    4 weak, absent

158. M1-3 lingual cingulum
    0 absent
    1 0/2
    2 weak, broken
    3 2/4
    4 strong, complete

159. convex distal lobe for M1-2 hypocone
    0 absent
    1 0/2
    2 present, distal crown margin weakly concave
    3 2/4
    4 present,_distal_crown_margin_deeply_notched

160. molar protocone lingual inflation (RM31-176)
    0 not inflated
    1 0/2
    2 slightly inflated
    3 2/4
    4 very inflated

161. lingual extension of M1 hypocone lobe
    0 lobe does not extend lingually far beyond protocone
    1 0/2
    2 lobe does extend far lingually past protocone

162. M1 mesiobuccal fovea delimited by trenchant parahypocrista
    0 absent
    1 0/2
    2 present

163. M2 buccal expansion of paracone (RM33-177)
    0 no expansion

1 0/2
2 slight expansion
3 2/4
4 considerable expansion

164. M2 postmetacrista
0 short,_indistinct,_or_absent
1 long,_trenchant,_and_labially_extended

165. M2 prehypocrista development (RM13-163)
0 absent
1 0/2
2 weak
3 2/4
4 strong_--_reaches_to_postprotocrista,_encloses_the_talon_lingually

166. M2 shape (bl/md)
0 very broad (>1.65)
1 0/2
2 broad_(<1.65,>1.30)
3 2/4
4 squared_(=<1.30)

167. shape of M2 centrocrista
0 straight, aligned with mesiodistal plane
1 0/2
2 crests are more buccally oriented, meet at an angle
3 2/4
4 crests meet at a sharp angle or form a mesostyle

168. M3 hypocone
0 absent or small
1 0/2
2 small
3 2/4
4 larage

169. M3 metacone
0 absent or very small
1 0/2
2 moderate (but smaller than paracone)
3 2/4
4 large (equal to paracone)

170. M3 paraconule (RM30-175)
0 absent

1 0/2
2 small-moderate
3 2/4
4 large

171. M3 relative to M1
0 very small (half or less of M1)
1 0/2
2 small (two thirds)
3 2/4
4 large (app same size)

172. M3 root number (RM2-153)

0 three
1 0/2
2 two
3 2/4
4 one

173. mandible fusion
0 absent
1 present

174. mandible angle
0 ventrally
1 postero-ventrally
2 hooks dorsally upward
3 widely expanded posteroventrally
4 mandibular angle very slight and low rugosity
5 0/1

175. mandibular depth (Y39,RCr45-227)
0 shallow_(less_than_1.8_times_as_deep_@_m2_as_md_length_of_m2)
1 0/2
2 deep_(>1.8_times_as_deep_@_m2_as_md_length_of_m2,_<2.19)
3 2/4
4 very_deep_(more_than_2.2_times_as_deep_@_m2_as_md_length_of_m2)

176. genial fossa
0 absent
1 present
2 0/1

177. posterior surface of condylar process

0 broad and slightly angled inferiorly [funnel-like]
1 globular
2 resembling a clock-wise rotated L such that the medial and dorsal aspects are thickened and the postero-lateral aspect is indistinct
3 medio-laterally broad and dorso-ventrally short
4 posterior aspect does not show a clear articular surface
5 polymorphic

178. height of coronoid process relative to condyle (RCr43-225)
0 very high above
1 slightly above or equal

179. shape of masseteric fossa
0 shallow
1 deeply excavated
2 intermediate
3 polymorphic

180. mandibular foramina
0 absent
1 present, one under incisor
2 present multiple anterior most under incisor
3 present multiple anteriormost lateral to lateral incisor
4 present, one lateral to incisor
5 2/3
6 3/4

181. mandibular lamina
0 absent
1 slight protuberence present
2 distinct notch-like protuberance prresent
3 0/1
4 1/2
5 0/1/2

182. mandibular symphysis tubercle
0 indistinct
1 distint
2 0/1

183. condyle height relative to toothrow (RCr44-226)
0 at level of toothrow
1 slightly above
2 well above toothrow

184. facial profile (Masters & Brothers, 2002)*

  0 straight
  1 0/2
  2 dished

185. degree of orbital convergence (contains information similar to RCr32-214)
  0 >89
  1 0/2
  2 90-104
  3 2/4
  4 105-119
  5 4/6
  6 120-134
  7 6/8
  8 >135

186. orbit size (contains information similar to RCr23-205)
  0 small
  1 large
  2 hypertrophied

187. pronounced interorbital constriction (RCr27-209)
  0 absent
  1 present below CN I

188. infraorbital foramina
  0 one
  1 two
  2 three
  3 0/1
  4 1/2

189. orbital orientation
  0 greatly flared
  1 acutely laterally flared
  2 180 degrees to midline
  3 acute lateral flare, dorsally oriented

190. length of infraorbital canal
  0 one-third the length of rostrum
  1 very short, almost just an opening through orbital rim from max to orbit
  2 intermediate
  3 1/2

191. ethmomaxillary fissure (Y13, modified following Cartmill 1978)
  0 absent
  1 present

2 0/1

192. anterior and posterior hiatus of ethmomaxillary fissure (Cartmill, 1978)
0 anterior hiatus variably present
1 0/2
2 posterior hiatus at least variably present
3 2/4
4 no hiatuses present

193. ascending wing of premaxilla
0 narrow
1 broad
2 0/1

194. rostral projection of premaxilla
0 absent
1 present
2 0/1

195. expansion of ethmoturbinals (YIP89)
0 no anteromedial expansion
1 anterior and medial expansion

196. transverse lamina/ethmoturbinal recess
0 extensive transverse lamina and ethmoturbinal recess present
1 extensive transverse lamina and ethmoturbinal recess absent

197. nasal morphology (Y62, contains information similar to R289)
0 lateral cleft between medial and lateral nasal processes
1 lateral cleft fused and rhinarium covered with dry hairy skin

198. nasal sinus swelling
0 absent
1 nasals swollen, causing inflated lacrimals
2 0/1

199. frontal-maxillary contact
0 present
1 0/2
2 absent due to intervening lacrimal
3 0/4
4 absent due to intervening premaxilla
5 absent due to orbital constriction

200. frontal-palatine contact (Cartmill 1978)
0 absent

1 present
2 0/1

201. lacrimal-palatine contact (RCr28-210)
0 present
1 no contact, separated by large front-max contact, or small os planum
2 no contact, separated by large os planum-maxillary contact
3 no contact, separated by ethmomaxillary fisure
4 0/1

202. zygomatic-lacrimal contact (Y6)
0 absent
1 present
2 0/1

203. lacrimal foramen (Y11)
0 surrounded by lacrimal bone
1 lies on lacrimal-maxillary suture
2 lac-max suture but is primarily surrounded by maxilla

204. position of lacrimal foramen (RCr30-212)
0 on_rim,_or_outside_of,_orbit_
1 inside the orbit

205. relation of infraorbital foramen to lacrimal (Tattersall and Schwartz 1999)
0 IOF lies in line with or posterior to LF
1 IOF anterior to LF
2 0/1

206. metopic fusion (RCr31-213)
0 absent
1 present
2 nearly fused, slight/faint suture
3 0/1
4 0/2
5 1/2
6 0/1/2

207. snout length (RCr37-219)
0 long snout
1 short snout

208. alisphenoid shape (Tattersall and Schwartz 1991)
0 concave
1 inflated
2 intermediate

3 0/2

209. ethmoid exposure in inner orbit (Cartmill 1978)
- 0 absent
- 1 present
- 2 0/1

210. exposure of maxilla laterally in orbital floor in superior view (Tattersall and Schwartz 1999)
- 0 extensively exposed laterally
- 1 moderately exposed
- 2 completely covered
- 3 maxilla drops off vertically in orbit so not exposed, but not covered

211. inflation of palatine in inner orbit (Tattersall and Schwartz 1999)
- 0 absent
- 1 present slight
- 2 present extreme
- 3 0/1
- 4 1/2

212. maxillary depth (RCr38-220)
- 0 deep
- 1 shallow

213. morphology of frontal segment of the postorbital bar (Y17, contains information similar to RCr24-25)
- 0 partial frontal process but no postorbital bar
- 1 slender and delicate
- 2 1/3
- 3 wide and robust
- 4 incorporated into postorbital septum

214. morphology of zygomatic portion of postorbital bar (Y18, contains information similar to RCr24-25)
- 0 no postorbital bar
- 1 slender and delicate
- 2 1/3
- 3 wide and robust
- 4 contributes to postorbital septum

215. inferior anterior zygomatic
- 0 thin and round
- 1 robust with flattened origin of masseter
- 2 intermediate
- 3 0/1
- 4 1/2

216. notch in inferior zygomatic
- 0 absent
- 1 present
- 2 0/1

217. nuchal crest development
- 0 absent
- 1 present weak
- 2 present marked
- 3 0/2
- 4 0/1
- 5 1/2
- 6 0/1/2

218. mastoid inflation (RCr3-185)
- 0 absent
- 1 present slight
- 2 present marked
- 3 0/1
- 4 1/2

219. parietal emissary foramina (Y33)
- 0 absent
- 1 0/2
- 2 present

220. sagittal cresting
- 0 temporal lines converge on frontal
- 1 0/2
- 2 temporal lines converge on parietals
- 3 temporal lines not confluent, subparallel, no crest
- 4 2/3
- 5 sag crest extensive, temporal lines converge on parietals
- 6 temporal lines not confluent, subparallel, no crest but temporal lines form raised distinct bony ridges
- 7 2/6

221. suprameatal foramen (RCr21-203)
- 0 absent
- 1 present,_small,_and_in_the_posterior_root_of_the_zygomatic_arch
- 2 present,_large,_and_above_the_external_auditory_meatus
- 3 0/2

222. shape of external auditory meatus
- 0 tubular

1 0/2
2 not tubular

223. postorbital bar/septum
0 frontal/zygomatic do not contact, no bar
1 frontal/zygomatic contact form a postorbital bar no septum
2 zygomatic/frontal/parietal contact contributes to septum

224. zygomatic arch depth
0 slender
1 0/2
2 dorsoventrally deep

225. zygomaticofacial foramen
0 absent
1 present small
2 present large
3 0/1
4 1/2

226. thickness of zygomatic portion of postorbital bar (quant)
227. Frontal length (quant)
228. Nasal length (quant)
229. postorbital constriction (quant)
230. Skull height (quant)
231. Occipital length (quant)
232. basal skull length (quant)
233. breadth of central basicranium (quant)
234. choanal shape (Tattersall and Schwartz 1999)
0 broad
1 peaked
2 0/1

235. position of the anteriormost point on the palatine/maxillary suture of the palate (Y19)
0 medial to space between M1 and M2 or more posterior
1 0/2
2 medial to M1
3 2/4
4 medial to the space between P4 and M1

236. position of the posteromedial edge of the palate in relation to M3 (Y24)
0 anterior to
1 medial to
2 posterior to M3
3 0/1
4 1/2

237. maxillary palatine notch, slight groove between the maxilla and palatine at approximate level of M3

0 absent
1 present

238. position of anterior palatine foramina relative to incisors (Masters & Brothers, 2002)*

0 foramina sit behind first incisors
1 0/2
2 foramina intrude between first incisors

239. cranial base behind hard palate

0 roof of nasal fossa and cranial base posterior to it form a continuous flat plane, the sphenoid continuing into the posterior part of the nasal fossa at the same level as sphenooccipital synchondrosis

1 roof of nasal fossa raised anterior to the level of the palatine, a steep plane forming in the sphenoid medially and palatine laterally

2 plane commences more posteriorly, such that ?post-choanal pits? are visibile posterior to the palate but mostly anterior to M3 and pterygoid plate

3 plane commences more posteriorly, at the level of the wing of the internal pterygoid plate

4 depression marked, with posterior excavation toward the occipital producing paired 'post-choanal pits'

5 0/1
6 1/2

240. posterior palatine flange

0 unextended posteriorly leaving the maxilla widely exposed in the posterior part of the orbital floor

1 short flange that extends slightly posteriorly, partly obscuring sphenopalatine foramen/maxilla

2 moderately to reach the edge of the temporal fossa
3 greatly intruding into the fossa
4 0/1
5 1/2
6 2/3

241. posterior palatine foramen

0 large, shallow and round
1 large, oval and canal-like
2 tiny/absent
3 moderate oval
4 1/3
5 0/2
6 2/3

242. number of palatine foramina
    0 absent
    1 one
    2 two
    3 three
    4 polymorphic

243. posterior palatine torus
    0 absent
    1 present
    2 0/1

244. basioccipital flange (contains information similar to RCr20-202)
    0 absent or minimal
    1 present,_extensive

245. paroccipital processes
    0 absent
    1 0/2
    2 present, small
    3 2/4
    4 present large

246. central stem of basicranium (D47)
    0 narrow
    1 broad

247. extent of contact between the lateral pterygoid plate and the bullar wall (RCr19-201)
    0 slight
    1 very extensive

248. lateral pterygoid-bulla
    0 absent
    1 abutting
    2 laminar
    3 0/1
    4 1/2
    5 0/2
    6 0/1/2

249. composition of bulla
    0 petrosal
    1 entotympanic

250. auditory bulla deflation
    0 inflated bony structures

1 deflated

251. epitympanic crest (RCr48-230)
 0 absent
 1 present

252. position of chorda tympani relative to m. tensor tympani (Maier, 2008)
 0 ventral to m. tensor tympani
 1 dorsal to m. tensor tympani
 2 m. tensor tympani absent

253. position of ventral edge of tympanic bone (RCr14-196)
 0 intrabullar
 1 extrabullar

254. entoglenoid proess
 0 indistinct absent
 1 0/2
 2 robust

255. encroachment of auditory bulla on pterygoid fossa (RCr17-199)
 0 absent
 1 present and formed by the AAC
 2 present and formed by the tympanic cavity
 3 1/2

256. postglenoid-auditory bullar relationship
 0 not confluent
 1 partially fused
 2 postglenoid process fused to lateral aspect of bulla
 3 0/1
 4 1/2

257. postglenoid process
 0 absent
 1 present

258. position of postglenoid foramen relative to postglenoid process
 0 posterior to postero-medial to postglenoid process
 1 medial to postglenoid process, abutting bulla
 2 foramen posteromedial to the postglenoid process but then surrounded by a bony lamina from the bulla
 3 fusion of process and bulla extensive and foramen located medial to process such that it is totally surrounded by bone
 4 0/1
 5 foramen absent

259. foramen ovale
- 0 lateral side of lateral pterygoid
- 1 posterior to terminus of lat pterygoid
- 2 medial to lateral ptery
- 3 0/1

260. foramen rotundum
- 0 absent, confluent with superior orbital fissure
- 1 present
- 2 0/1

261. mediolateral position of carotid
- 0 medial
- 1 midline of bulla
- 2 lateral
- 3 1/2

262. basisphenoid foramen between pterygoid plate
- 0 absent
- 1 present
- 2 0/1

263. medial vs lateral pterygoid depth
- 0 shorter than
- 1 approximately equal to
- 2 deeper than
- 3 0/1
- 4 1/2

264. presence or absence of canal for internal carotid artery or nerves (RCr13-195)
- 0 absent
- 1 present

265. ventrodorsal position of posterior carotid foramen relative to fenestra cochleae (RCr7-189)
- 0 dorsal
- 1 ventral

266. rostrocaudal position of posterior carotid foramen with respect to fenestra cochleae (contains information similar to RCr8-190)
- 0 posterior to fenestra cochleae
- 1 ventral to fenestra cochleae
- 2 anterior to fenestra cochleae

267. morphology of promontory canal
- 0 absent

1 open trough
2 complete canal

268. morphology of annular bridge (RCr16-198)
0 linea semicircularis or partial anular bridge formed on an entotympanic bulla
1 linea semicircularis formed on a petrosal bulla
2 complete annular bridge

269. parotic fissure (RCr22-204)
0 patent
1 closed

270. perbullar pathway for internal carotid artery (RCr4-186)
0 absent
1 present

271. position of ectotympanic
0 ring-like ectotympanic lies within the bulla and is free at the bottom when looking inside EAM
1 ectotympanic ring-like and fused to lateral aspect of bulla
2 ectotympanic tube-like and fused to lateral aspect

272. position of infraorbital foramina (contains information similar to Y3)
0 above P2
1 0/2
2 above P3
3 2/4
4 above P4
5 4/6
6 above M1

273. position of pathway for internal carotid artery or nerve relative to fenestra cochleae (RCr9-191)
0 runs_across_ventral_lip_of_fenestra_cochleae,_shielding_it_from_ventral_view
1 does not shield fenestra cochleae

274. position of pyramidal processes (RCr35-217)
0 medially placed
1 0/2
2 laterally placed

275. position of sphenopalatine foramen
0 within palatine
1 0/2
2 on ethmopalatine suture

276. transverse septum defining caudal wall of anterior accessory cavity (contains information similar to RCr1-183)

    0 absent
    1 present,_forms_lateral_wall_of_AAC_pneumatized_from_tympanic_cavity
    2 present,_forms_lateral_wall_of_AAC_pneumatized_from_epitympanic_recess

277. trabeculated anterior accessory cavity

    0 absent
    1 present

278. shape of medial pterygoid plate (RCr36-218, contains information similar to Y22)

    0 long_medial_pterygoid_plate_extending_one-third_to_one_half_of_the_distance_to_the_anterior_surface_of_the_bulla
    1 0/2
    2 short but distinct from lateral pterygoid plate for its entire dorsoventral extent
    3 2/4
    4 medial_pterygoid_plate_entirely_absent,_or_reduced_to_a_low_rugosity

279. Scapular morphology (mediolateral width/inferosuperior height)

    0 <1.25
    1 0/2
    2 <1.5-1.25
    3 2/4
    4 >1.5,<1.75
    5 4/6
    6 >1.75

280. relative size of infra and supraspinous fossae

    0 supraspinous fossa larger than infraspinous fossa
    1 0/2
    2 fossae roughly equivalent
    3 2/4
    4 infraspinous fossa approximately two times as large as the supraspinous fossa
    5 4/6
    6 infraspinous fossa approximately three times as large as the supraspinous fossa

281. teres major insertion

    0 absent or poorly defined
    1 0/2
    2 elongate, well defined crest
    3 2/4
    4 well developed tubercle

282. shape of glenoid

    0 wide and biconcave
    1 anteroposteriorly oriented trough

283. shape of humeral trochlea
    0 cylindrical,_distomedial_aspect_of_trochlea_is_straight
    1 0/2
    2 conical,_medial_aspect_of_trochlea_flares_distally

284. supinator crest
    0 prominent
    1 low

285. shape of dorsal aspect of distal humeral articulation (contains information similar to that of RH10-241)
    0 no pronounced lips on dorsal trochlear edges
    1 0/2
    2 both medial and lateral edges pronounced
    3 very pronounced lateral lip

286. brachialis flange
    0 broad
    1 0/2
    2 moderate
    3 2/4
    4 narrow

287. morph of deltopectoral crest
    0 prominent
    1 0/2
    2 low

288. dorsal placement of medial epicondyle
    0 parallel
    1 0/2
    2 slight dorsal angle
    3 2/4
    4 large dorsal angle

289. dorsoepitrochlear fossa
    0 present
    1 0/2
    2 small, shallow
    3 2/4
    4 absent

290. humeral head relative to tubercles
    0 humeral head is expanded dorsal to tubercles
    1 0/2

2 humeral head and tubercles are approximately equal in height
3 2/4
4 tubercles are expanded above humeral head

291. humerofemoral index
0 <59
1 0/2
2 60-69
3 2/4
4 70-79
5 4/6
6 80-89
7 6/8
8 90-100

292. length of scapular coracoid process (coracoid process length/glenoid fossa height)
0 <=0.9
1 0/2
2 >.9-1
3 2/4
4 >1, <1.1
5 4/6
6 >1.1

293. olecranon fossa morphology (Y78, contains information similar to RH12-243)
0 deep,_open_and_unossified_
1 0/2
2 moderately_deep,_thinly_ossified_and_nearly_transparent_
3 2/4
4 shallow, robustly ossified

294. presence/mediolateral position entepicondylar
0 foramen is placed far proximal to trochlea
1 0/2
2 lateral wall of medial strut defining foramen is confluent with medial edge of the trochlea
3 foramen_more_medial,_and_lateral_wall_of_medial_strut_defining_foramen_is_not_confluent_with_medial_edge_of_the_trochlea
4 absent

295. relative heights of medial and lateral edges of the humeral trochlea (RH2-233)
0 subequal
1 0/2
2 medial edge more flared than lateral edge

296. rotation of medial malleolus

0 none
1 0/2
2 slight
3 2/4
4 strong

297. second digit of hand

0 of normal length
1 drastically reduced

298. medial epicondyle

0 reduced
1 0/2
2 prominent

299. shape of the medial malleolar articular surface (RT5-266)

0 flat
1 0/2
2 anteriorly_convex,_posteriorly_flat
3 2/4
4 all convex

300. ulnar-pisiform articulation

0 no_ulnar-pisiform_articulation
1 facet_on_pisiform_for_ulnar_styloid_process_is_smaller_than,_or_roughly_equal_in_size_to,_that_for_triquetrum
2 facet on pisiform for ulnar styloid process is much enlarged and deeply excavated

301. trochlear-capitular junction

0 trochlea_and_capitulum_are_confluent,_with_no_distinct_trochleo-capitular_ridge
1 0/2
2 lateral aspect of trochlea is offset from capitulum by a weak ridge
3 2/4
4 lateral aspect of trochlea is separated from capitulum by a deep gutter

302. capitular shape

0 globular
1 0/2
2 ovoid

303. capitular tail

0 elongate and distinct
1 short or absent
2 1/3

- 3 proximodistally tall capitular flange is present

304. styloid process
- 0 no discernable styloid process
- 1 present but only moderately developed
- 2 long_and_well-developed_

305. size of centrale, orientation of centrale trapezoid facet, and articulation with hamate (modified from RW1-249)
- 0 facet_faces_distally,_no_articulation_with_hamate
- 1 facet_faces_distoradially,_articulation_with_hamate
- 2 centrale not present as an independent element

306. navicular length relative to width (contains information similar to RN1-278)
- 0 <100
- 1 100-150
- 2 >150% longer than wide

307. morphology of the naviculocuboid articulation (RN3-279)
- 0 cuboid facet contacts only the ectocuneiform
- 1 cuboid facet contacts the ectocuneiform and the mesocuneiform

308. three-pronged distal navicular articulation
- 0 absent
- 1 present

309. femoral head shape
- 0 spherical
- 1 semicylindrical
- 2 cylindrical

310. morphology of femoral head articular surface
- 0 restricted to femoral head
- 1 extends onto back of femoral head

311. fovea capitis
- 0 small insignificant
- 1 0/2
- 2 present, well developed

312. length of femoral neck
- 0 <=75
- 1 0/2
- 2 >75<120
- 3 2/4
- 4 >120

313. crista paratrochanterica
- 0 absent
- 1 0/2
- 2 present

314. anteroposterior angulation of proximal femur (contains information similar to RF8-258)
- 0 bent anteriorly
- 1 not bent anteriorly

315. triangular depression on medial side of proximal femur (Dagosto and Schmid, 1996)
- 0 absent
- 1 present

316. gluteal tuberosity
- 0 present, large
- 1 0/2
- 2 present, small reduced crest
- 3 2/4
- 4 absent

317. position of gluteal tuberosity
- 0 proximal to lesser trochanter
- 1 0/2
- 2 at level of lesser trochanter
- 3 2/4
- 4 distal to lesser trochanter

318. angle of femoral neck
- 0 <60
- 1 0/2
- 2 60-70
- 3 2/4
- 4 >70

319. angle of lesser trochanter (RF3-253)
- 0 medial_(0-30_degrees)
- 1 0/2
- 2 posterior_(>30_degrees)

320. greater trochanter
- 0 hook-shaped
- 1 0/2
- 2 rounded

321. intertrochanteric crest (RF10-260)

0 absent
1 present

322. knee index (contains information similar to RF5-255)
0 100 or higher
1 90-99
2 80-89
3 70-79

323. patellar margin asymmetry
0 absent
1 present

324. relative length of trochanteric fossa
0 >125 (long)
1 0/2
2 110-125 (moderate)
3 2/4
4 <110 (very short)

325. retroflexion of proximal tibial articulation
0
absent,_articular_surface_of_tibial_condyles_perpendicular_to_long_axis_of_tibial_shaft
1 moderate retroflexion present
2 proximal articular surface is strongly retroflexed

326. position of tibialis posterior groove (RT7-268)
0 on medial side of malleolus
1 0/2
2 on posterior side of malleolus

327. shape of distal surface of tibia
0 square
1 intermediate
2 triangular

328. tibial process for peroneus longus
0 absent or poorly developed
1 present and distinct

329. shape of distal tibial shaft (RT6-267)
0 no compression
1 anteroposteriorly compressed

330. fusion of tibia and fibula (RT1-263)
0 absent,_small_articulation

1 no_fusion,_moderate_articulation
2 no fusion but extensive articulation
3 fusion

331. length of MT1 relative to MT3 (RMT2)
0 less than 70% the length of MT3
1 0/2
2 71-80%
3 2/4
4 81-90%
5 4/6
6 91-100%
7 6/8
8 >100%

332. metatarsus length (MT3 length/proximal phalanx of digit III) (contains information similar to that of RO4-285)
0 <1.0
1 0/2
2 >1.01,_<1.5
3 2/4
4 >1.51,_<2.0
5 4/6
6 >2.01

333. MTI distal articular surface midline keel
0 single
1 bifurcate

334. MTI distal epicondyle asymmetry in distal and dorsal views
0 medial epicondyle larger
1 epicondyles symmetrical
2 lateral epicondyle larger

335. MTI dorsal extension of proximal articular surface
0 present
1 absent

336. MTI dorsal notch located proximal to the distal articular surface in dorsal or lateral view
0 deep
1 intermediate
2 shallow

337. MTI dorsoplantar axis of head orientation relative to long axis of diaphysis in plantar view, with respect to the distal end of the bone
0 medial

1 intermediate
2 lateral

338. MTI head distal projection in dorsal view
0 short
1 long

339. MTI head shape in distal view
0 ovoid
1 rectangular

340. MTI medial proximally projecting tubercle size
0 smaller or equal in size to peroneal process
1 larger than peroneal process

341. MTI medial side of proximal articular surface with respect to the proximal end of the bone
0 rounded or weak keel
1 strong keel

342. MTI peroneal process dorsoplantar thickness in dorsolateral view with respect to the proximal end of the bone
0 flat
1 shallow
2 deep

343. MTI proximal articular surface angle, in dorsolateral view with respect to the proximal end of the bone
0 <=105
1 >105

344. MTI proximal articular surface notch location
0 absent
1 medioplantar
2 lateroplantar

345. MTI proximal articular surface orientation in proximal view (i.e., torsion)
0 dorsoventral
1 0/2
2 intermediate
3 2/4
4 mediolateral

346. MTI proximal articular surface shape in dorsolateral view
0 slight concavity
1 deep concativty, saddle-shaped

347. MTI relative dorsoplantar diaphysis midshaft breadth
    0 wide
    1 narrow

348. peroneal tubercle shape
    0 discrete tubercle with clearly defined borders
    1 tubercle gradually slopes into body (substantially longer proximodistally relative to mediolateral width)

349. position of distal terminus of ectal facet relative to anterior calcaneal segment
    0 dorsally positioned on body
    1 intermediate condition
    2 sunk into body plantarly

350. position of groove for flexor fibularis (RA1-269)
    0 lateral to astragalar trochlea
    1 plantar to astragalar trochlea

351. position of peroneal process relative to sustentaculum
    0 below
    1 lower half
    2 upper half

352. morphology of groove for flexor fibularis under sustentaculum
    0 no noticeable groove present
    1 deep medially with distinct groove or wall

353. size of lateral tubercle buttressing flexor fibularis
    0 poorly developed
    1 0/2
    2 small
    3 2/4
    4 large

354. level of distal plantar tubercle (tubercle to cuboid facet/calcaneal length)
    0 distal, near cuboid facet (0-0.19)
    1 more proximal (>0.20)

355. fibular facet angle
    0 79 degrees or less
    1 0/2
    2 80-89
    3 2/4
    4 90-99
    5 4/6
    6 100-109

7 6/8
8 110+

356. foot axis (R01-282)
    0 mesaxonic
    1 paraxonic
    2 ectaxonic

357. concavity of cuboid facet
    0 flat (>=160
    1 shallow (>=150, <160
    2 deep (<150)

358. development of distal plantar tubercle on calcaneus
    0 small,_poorly_developed
    1 0/2
    2 well-developed

359. dorsal extension of bone supporting cuboid facet
    0 absent
    1 present

360. dorsal heel process
    0 tucked under ectal facet in lateral view
    1 level with ectal facet in lateral view
    2 projects dorsal to ectal facet

361. ectal facet flange development
    0 absent
    1 intermediate
    2 present

362. ectal facet radius of curvature
    0 <120 degrees
    1 >=120 degrees

363. shape of medial edge of sustentaculum in plantar view
    0 triangular or beak-like
    1 rounded

364. relative length of ectal facet (ectal facet width/ectal facet length)
    0 <50
    1 0/2
    2 >50,_<60
    3 2/4
    4 >60

365. facet anterior to the anterior extension of the sustentacular facet (navicular or otherwise)
0 prominent
1 very small or absent

366. form of medial margin between sustentaculum and anterior calcaneal facet (viewed dorsally)
0 waisted into body
1 relatively linear medial margin

367. angle between sustentaculum and ectal facet
0 <140
1 140-160
2 >160-<180
3 >180

368. position of the peroneal tubercle relative to ectal facet (RC2-276)
0 maximum width of peroneal tubercle is placed distal to distal terminus of ectal facet
1 maximum width of peroneal tubercle is placed approximately at the distal terminus of the ectal facet
2 maximum width of peroneal tubercle is placed proximal to the distal terminus of the ectal facet, closer to the distal terminus of the ectal facet than the proximal
3 maximum width of peroneal tubercle is placed proximal to distal terminus of the ectal facet, closer to the proximal terminus of the ectal facet than distal

369. lateral process of entocuneiform (RE2-281)
0 small
1 hypertrophied

370. nail/claw on second pedal digit (Y82,RO2-283)
0 nail present
1 claw present

371. prehallux
0 present
1 absent

372. shape of intertubercular sulcus (contains information similar to RH15-246)
0 narrow and deep
1 0/2
2 narrow and shallow
3 2/4
4 shallow and wide

373. relative width of capitulum (contains information similar to RH5-236)
0 ventral_articular_width/capitular_width_>2.5

1 0/2
2 <2.5,_>2.0
3 2/4
4 <2.0

374. number of "peaks" on calcaneal peroneal tubercle
0 single tubercle present
1 two "peaks" present

375. proximal calcaneal elongation (length from proximal border of ectal facet to proximal end of calcaneus/calcaneus length) from Gebo et al. 2001
0 .10-.15
1 0/2
2 .16-.20
3 2/4
4 .21-.25
5 4/6
6 .26-.30
7 6/8
8 >.31

376. orientation of long axis of calcaneocuboid joint
0 dorsoventral
1 oblique
2 mediolateral

377. posterior (plantar) calcaneal bowing
0 absent
1 present, moderately developed
2 present, extreme bowing

378. mediolateral bowing of calcaneal tuber
0 absent
1 present, moderate bowing
2 present, extreme bowing

379. anterior calcaneal elongation (length of calcaneus distal to ectal facet/total calcaneal length x 100) (modified from RC1-275, scoring from D22 addendum)
0 >30,<40
1 0/2
2 >41,<50
3 2/4
4 >51,<60
5 4/6
6 >61,<70
7 6/8

8 >71

380. bony distinction between plantar edge of ectal facet and body
  0 no well-defined border
  1 well-defined border present

381. calcaneal sustentacular facet configuration
  0 single continuous sustentacular facet present
  1 0/2
  2 separate anterior and posterior sustentacular facets present

382. calcaneal width/length
  0 <35
  1 0/2
  2 >35<40
  3 2/4
  4 40-45
  5 4/6
  6 45-50
  7 6/8
  8 >50

383. calcaneocuboid joint shape
  0 oval
  1 fan-shaped noth is articular
  2 fan-shaped notch is non-articular
  3 oval but longest in dorsoplantar direction

384. shape of tuber calcanei
  0 oval
  1 square/rectangular
  2 uneven walls/trapezoidal
  3 proximally projecting medial wall

385. size of tuber calcanei
  0 relatively small (sliver, oval, no clear insertion for tendo calcanei)
  1 medium (large in one direction, insertion for tendo calcanei present but not robust)
  2 relatively large

386. size of calcaneal peroneal tubercle (100*widest point on peroneal tubercle to ectal facet, measured perpendicular to long axis of bone/calcaneal width)
  0 massive, extends far laterally (>=21)
  1 medium (<21)
  2 highly reduced or too small to measure

387. astragalar body height

0 <100
1 0/2
2 100-120
3 2/4
4 >120

388. astragalar cotylar fossa (Seiffert & Simons, 2001)
0 shallow
1 0/2
2 moderate
3 2/4
4 deep,_medially_projecting

389. astragalar neck angle
0 <20 degrees
1 0/2
2 20-30 degrees
3 2/4
4 >30 degrees

390. astragalar neck length
0 <100
1 0/2
2 >100<120
3 2/4
4 >120

391. astragalar width/astragalar length
0 <50
1 0/2
2 >50<60
3 2/4
4 >60<70
5 4/6
6 >70

392. elevated lateral trochlear margin of astragalus
0 absent
1 0/2
2 present

393. plantarflexion of astragalar head*
0 absent
1 present

394. relative astragalar head width

0 head_width/head_height_x_100_<115
1 0/2
2 head_width/head_height_x_100_>115,_<130
3 2/4
4 head_width/head_height_x_100_>130

395. posterior astragalar shelf (D20; contains information similar to RA4-272)
0 absent
1 0/2
2 present small
3 2/4
4 present large

396. shape of proximal aspect of medial tibial facet on astragalus (RA6-274, modified)
0 dorsoventrally_deep,_extends_to_plantar_aspect_of_astragalus
1 0/2
2 dorsoventrally_restricted,_confined_to_dorsal_half_of_astragalar_body

397. number of thoraco-lumbar vertebrae
0 17 or fewer
1 0/2
2 18
3 2/4
4 19
5 4/6
6 20
7 6/8
8 21 or more

398. anticlinal vertebra
0 T10
1 T11
2 T12
3 L1
4 no anticlinal vertebra

399. spinous process reduction on thoraco-lumbar vertebrae
0 distinct, elongate processes, no reduction
1 reduced and indistinct

400. transpedicular foramina
0 absent
1 present

401. shape of manubrium
0 sternal head elongate

1 shortened and triangular

402. sacral vertebrae
    0 2-3
    1 4-5
    2 >5

403. pubic bone flaring
    0 absent
    1 present

404. ilium shape
    0 narrow
    1 0/2
    2 markedly flared

405. anterior inferior iliac spine
    0 tuberosity not expressed
    1 small tubercle
    2 well developed tuberosity present

406. ischial flaring
    0 absent
    1 present

407. tail length (Y86)
    0 long tail
    1 reduced
    2 absent

408. ascorbic acid synthesis
    0 absent
    1 present

409. tapetum lucidum (Y59, R290)
    0 present
    1 absent

410. retinal fovea (Y60, R288)
    0 absent
    1 present

411. allantois development (KPL6)
    0 large,_vesicular
    1 rudimentary

412. amniotic cavity (KPL3)
    0 primordial cavity absent
    1 primordial cavity present

413. presence/absence of choriovitelline placenta (Y58, KPL4)
    0 choriovitelline placenta
    1 no choriovitelline placenta

414. embryonic body stalk (KPL5)
    0 absent
    1 present

415. epitheliochorial vs. hemochorial placentation (KPL1)
    0 epitheliochorial
    1 diffuse,_hemochorial

416. ascending pharyngeal artery (Y52)
    0 if present is poorly developed
    1 present and enlarged

417. blastocyst attachment (KPL2)
    0 invasive
    1 non-invasive

418. stapedial
    0 extremely small undetectable
    1 present

419. relative size of stapedial and promontory arteries (contains information similar to RCr11-193)
    0 equal size
    1 stapedial smaller than promontory
    2 stapedial absent or reduced
    3 promontories present, stapedials larger
    4 both absent
    5 1/2
    6 1/3

420. retia mirabilia of the proximal limb vessels (YIP87)
    0 absent
    1 present

421. vascular plexus associated with ascending pharyngeal artery (Y53)
    0 absent
    1 present

Supplemental Information Table 1. Percent missing data in the complete (421) morphological character matrix

Binomial name	**proportion of missing data**
Adapis parisiensis	12%
Aegyptopithecus zeuxis	28%
Allenopithecus nigroviridis	13%
Alouatta seniculus	11%
Altiatlasius koulchii	90%
Anchomomys frontanyensis	69%
Aotus trivirgatus	10%
Archaeoindris fontoynontii	71%
Archaeolemur edwardsi	55%
Archaeolemur majori	88%
Arctocebus calabarensis	12%
Avahi laniger	58%
Avahi occidentalis	75%
Babakotia radafolia	60%
Branisella boliviana	67%
Cantius abditus	40%
Carpolestes simpsoni	21%
Cheirogaleus major	1%
Cynocephalus volans	60%
Daubentonia madagascariensis	58%
Daubentonia robustus	91%
Djebelemur martinezi	65%
Donrussellia provincialis	71%
Eulemur albifrons	57%
Eulemur fulvus	57%
Eulemur rufus	57%
Galagoides demidoff	1%
Galago moholi	11%
Galago senegalensis	78%
Hadropithecus stenognathus	62%
Hapalemur griseus	56%
Hapalemur simus	56%
Indri indri	54%
Karanisia clarki	69%
Komba robustus	61%

Lemur catta	1%
Lepilemur dorsalis	57%
Lepilemur edwardsi	56%
Lepilemur leucopus	55%
Lepilemur mustelinus	4%
Lepilemur ruficaudatus	56%
Leptadapis magnus	20%
Loris tardigradus	2%
Megaladapis edwardsi	59%
Megaladapis grandidieri	84%
Megaladapis madagascariensis	74%
Mesopropithecus dolichobrachion	68%
Mesopropithecus pithecoides	67%
Microcebus griseorufus	75%
Microcebus murinus	10%
Microcebus rufus	56%
Mirza coquereli	57%
Notharctus pugnax	95%
Notharctus tenebrosus	55%
Nycticeboides simpsoni	67%
Nycticebus bengalensis	78%
Nycticebus coucang	8%
Otolemur crassicaudatus	2%
Otolemur garnetti	78%
Pachylemur insignis	75%
Varecia variegata	2%
Palaeopropithecus ingens	72%
Palaeopropithecus maximus	63%
Pan troglodytes	12%
Perodicticus potto	3%
Phaner furcifer	57%
Plesiadapis tricuspidens	19%
Plesiopithecus teras	59%
Pronycticebus gaudryi	54%
Propithecus candidus	58%
Propithecus coquereli	58%
Propithecus coronatus	58%
Propithecus deckenii	58%
Propithecus diadema	59%
Propithecus edwardsi	61%

Propithecus perrieri	64%
Propithecus tattersalli	63%
Propithecus verreauxi	3%
Purgatorius unio	70%
Saharagalago misrensis	90%
Saimiri sciureus	10%
Tarsius bancanus	11%
Teilhardina americana	67%
Tupaia glis	1%
Wadilemur elegans	70%

Supplemental Information File 1. Morphological data matrix. Deposited in online database MorphoBank (www.morphobank.org, project # 2167).
Supplemental Information File 2. Concatenated partitioned molecular data alignment. Deposited in online database MorphoBank (www.morphobank.org, project # 2167).
Supplemental Information. Molecular data partitioning scheme from PartitionFinder:
model selection : bic
search : greedy
Best partitioning scheme
Scheme lnL : -75411.1184
Scheme BIC : 155074.251281
Number of params : 491
Number of sites : 5767
Number of subsets : 2

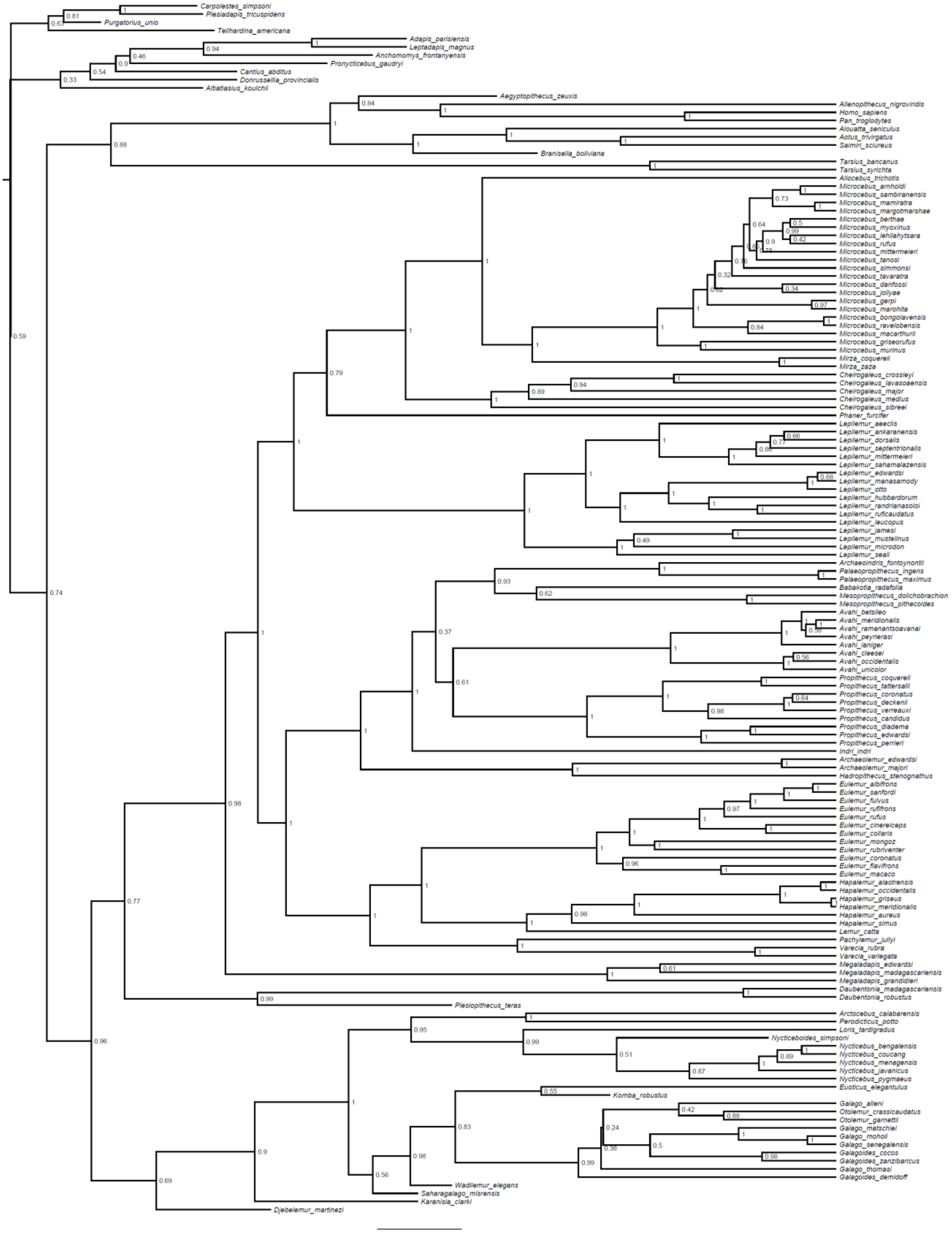
Subset	**Best Model**	**Subset Partitions**
1	SYM+I+G	ADORA pos[a]1, ADORA pos2, ADORA pos3, CNR pos1, CNR pos2, CNR pos3, ND4 pos2, ND4 pos3, RAG1 pos1, RAG1 pos2, RAG1 pos3, RAG2 pos1, RAG2 pos2, RAG2 pos3, cytb pos1, cytb pos2
2	GTR+I+G	ND4 pos1, cytb pos3

[a] Pos: codon position 1, 2, or 3.

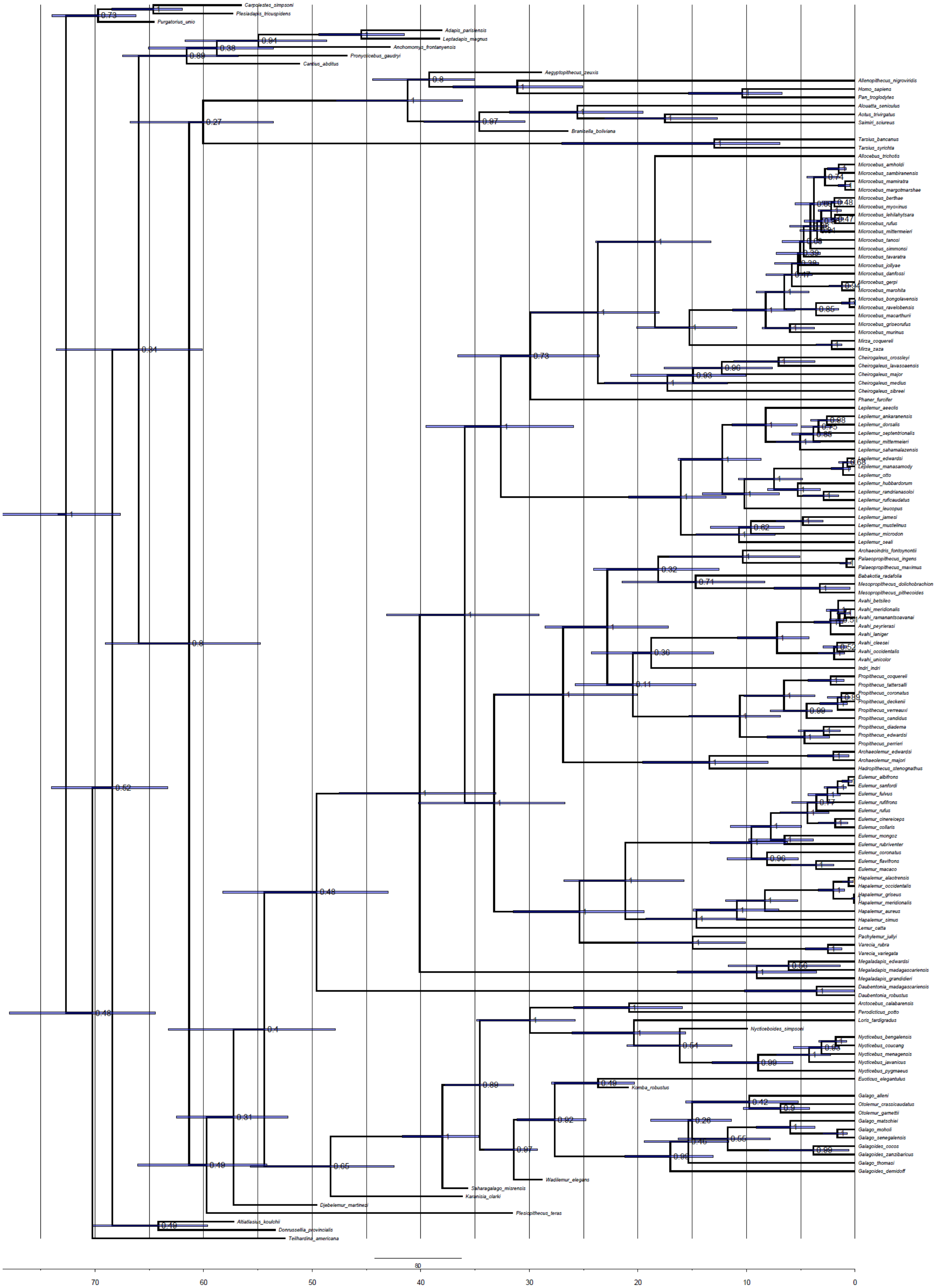
RaxML-style partition definitions:
DNA, p1 = 1-1139\3, 2-1139\3, 1141-2518\3, 1142-2518\3, 2519-2931\3, 2520-2931\3, 2521-2931\3, 2932-3931\3, 2933-3931\3, 2934-3931\3, 3932-5008\3, 3933-5008\3, 3934-5008\3, 5009-5767\3, 5010-5767\3, 5011-5767\3
DNA, p2 = 3-1139\3, 1140-2518\3

Supplemental Information 6. MrBayes block of code to run fossilized birth-death process and tip-dating analyses. Deposited in online database MorphoBank (www.morphobank.org, project # 2167).

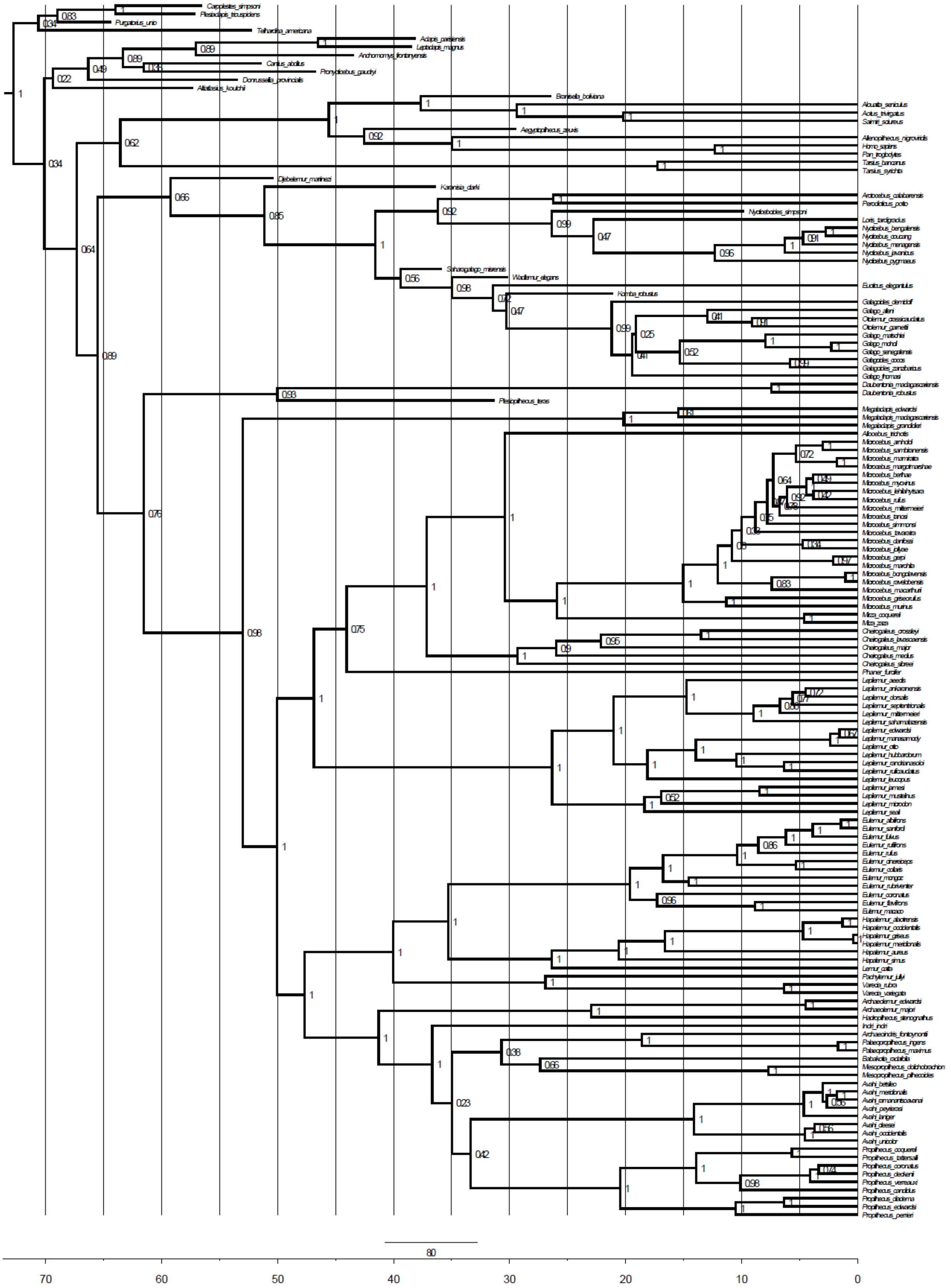
Supplemental Information Figure 1. Maximum clade credibility tree from tip-dating with 421 morphological characters and 5767 molecular characters. Posterior probabilities of nodes are labelled.



Supplemental Information Figure 2. Maximum clade credibility tree from fossilized birth-death process with 369 morphological characters and 5767 molecular characters. Posterior probabilities of nodes are labelled and the 95% highest posterior distribution of the node ages are illustrated.


Carpolestes_simpsoni
Plesiadapis_tricuspidens
Purgatorius_unio
Adapis_parisiensis
Leptadapis_magnus
Anchomomys_frontanyensis
Pronycticebus_gaudryi
Cantius_abditus
Aegyptopithecus_zeuxis
Allenopithecus_nigroviridis
Homo_sapiens
Pan_troglodytes
Alouatta_seniculus
Aotus_trivirgatus
Saimiri_sciureus
Branisella_boliviana
Tarsius_bancanus
Tarsius_syrichta
Allocebus_trichotis
Microcebus_arnholdi
Microcebus_sambiranensis
Microcebus_mamiratra
Microcebus_margotmarshae
Microcebus_berthae
Microcebus_myoxinus
Microcebus_lehilahytsara
Microcebus_rufus
Microcebus_mittermeieri
Microcebus_tanosi
Microcebus_simmonsi
Microcebus_tavaratra
Microcebus_jollyae
Microcebus_danfossi
Microcebus_gerpi
Microcebus_marohita
Microcebus_bongolavensis
Microcebus_ravelobensis
Microcebus_macarthurii
Microcebus_griseorufus
Microcebus_murinus
Mirza_coquereli
Mirza_zaza
Cheirogaleus_crossleyi
Cheirogaleus_lavasoaensis
Cheirogaleus_major
Cheirogaleus_medius
Cheirogaleus_sibreei
Phaner_furcifer
Lepilemur_aeeclis
Lepilemur_ankaranensis
Lepilemur_dorsalis
Lepilemur_septentrionalis
Lepilemur_mittermeieri
Lepilemur_sahamalazensis
Lepilemur_edwardsi
Lepilemur_manasamody
Lepilemur_otto
Lepilemur_hubbardorum
Lepilemur_randrianasoloi
Lepilemur_ruficaudatus
Lepilemur_leucopus
Lepilemur_jamesi
Lepilemur_mustelinus
Lepilemur_microdon
Lepilemur_seali
Archaeoindris_fontoynontii
Palaeopropithecus_ingens
Palaeopropithecus_maximus
Babakotia_radafolia
Mesopropithecus_dolichobrachion
Mesopropithecus_pithecoides
Avahi_betsileo
Avahi_meridionalis
Avahi_ramanantsoavanai
Avahi_peyrierasi
Avahi_laniger
Avahi_cleesei
Avahi_occidentalis
Avahi_unicolor
Indri_indri
Propithecus_coquereli
Propithecus_tattersalli
Propithecus_coronatus
Propithecus_deckenii
Propithecus_verreauxi
Propithecus_candidus
Propithecus_diadema
Propithecus_edwardsi
Propithecus_perrieri
Archaeolemur_edwardsi
Archaeolemur_majori
Hadropithecus_stenognathus
Eulemur_albifrons
Eulemur_sanfordi
Eulemur_fulvus
Eulemur_rufifrons
Eulemur_rufus
Eulemur_cinereiceps
Eulemur_collaris
Eulemur_mongoz
Eulemur_rubriventer
Eulemur_coronatus
Eulemur_flavifrons
Eulemur_macaco
Hapalemur_alaotrensis
Hapalemur_occidentalis
Hapalemur_griseus
Hapalemur_meridionalis
Hapalemur_aureus
Hapalemur_simus
Lemur_catta
Pachylemur_jullyi
Varecia_rubra
Varecia_variegata
Megaladapis_edwardsi
Megaladapis_madagascariensis
Megaladapis_grandidieri
Daubentonia_madagascariensis
Daubentonia_robustus
Arctocebus_calabarensis
Perodicticus_potto
Loris_tardigradus
Nycticeboides_simpsoni
Nycticebus_bengalensis
Nycticebus_coucang
Nycticebus_menagensis
Nycticebus_javanicus
Nycticebus_pygmaeus
Euoticus_elegantulus
Komba_robustus
Galago_alleni
Otolemur_crassicaudatus
Otolemur_garnettii
Galago_matschiei
Galago_moholi
Galago_senegalensis
Galagoides_cocos
Galagoides_zanzibaricus
Galago_thomasi
Galagoides_demidoff
Wadilemur_elegans
Saharagalago_misrensis
Karanisia_clarki
Djebelemur_martinezi
Plesiopithecus_teras
Altiatlasius_koulchii
Donrussellia_provincialis
Teilhardina_americana
80
70
60
50
40
30
20
10
0

Supplemental Information Figure 3. Maximum clade credibility tree from tip-dating method with 369 morphological characters and 5767 molecular characters posterior probabilities of nodes are labelled. See separate file.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Lepilemur_dorsalis
Lepilemur_septentrionalis
Lepilemur_mittermeieri
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Lepilemur_edwardsi
Lepilemur_manasamody
Lepilemur_otto
Lepilemur_hubbardorum
Lepilemur_randrianasoloi
Lepilemur_ruficaudatus
Lepilemur_leucopus
Lepilemur_jamesi
Lepilemur_mustelinus
Lepilemur_microdon
Lepilemur_seali
Eulemur_albifrons
Eulemur_sanfordi
Eulemur_fulvus
Eulemur_rufifrons
Eulemur_rufus
Eulemur_cinereiceps
Eulemur_collaris
Eulemur_mongoz
Eulemur_rubriventer
Eulemur_coronatus
Eulemur_flavifrons
Eulemur_macaco
Hapalemur_alaotrensis
Hapalemur_occidentalis
Hapalemur_griseus
Hapalemur_meridionalis
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Avahi_ramanantsoavanai
Avahi_peyrierasi
Avahi_laniger
Avahi_cleesei
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Avahi_unicolor
Propithecus_coquereli
Propithecus_tattersalli
Propithecus_coronatus
Propithecus_deckeni
Propithecus_verreauxi
Propithecus_candidus
Propithecus_diadema
Propithecus_edwardsi
Propithecus_perrieri
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10
0

Supplementary Information Table 2. Table of median node age estimates and range of 95% highest probability density distributions (in millions of years before the present) for key nodes in the primate phylogeny inferred using the fossilized birth-death process using wide (FBD1) or fixed point (FBD2) calibration priors and the tip-dating (TD) methods.

Node	**FBD1**	**error**	**FBD2**	**error**	**TD**	**error**
Plesiadapiformes/Euprimates	72.68	12.13	73.64	12.43	72.79	10.19
Haplorrhini/Strepsirrhini	61.34	14.29	62.75	16.24	67.32	13.36
Haplorrhini	60.04	13.17	61.9	14.45	63.56	14.53
Anthropoidea	41.21	11.62	42.23	10.86	45.58	11.51
Homo/*Pan*	10.39	6.62	10.46	8.17	12.29	9.55
Strepsirrhini	59.73	11.89	52.83	14.5	65.52	14.47
Lorisidae/Galagidae	34.57	6.36	37.42	6.05	41.57	8.34
African/Asian Lorisidae	29.96	9.1	32.29	16.54	36.18	9.61
Lemuriformes	49.58	15.21	48.26	17.11	61.54	13.54
Megaladapidae	40.13	14.44	41.35	15.83	53	12.56
Lemuridae/Indroidea	33.25	13.49	34.29	14.35	47.69	11.61
Lemuridae	25.38	12.05	25.38	12.95	20.12	11.43
-Eulemur	9.56	7.14	9.8	7.67	19.6	13.06
Indroidea/Archaeolemuridae	26.89	13	27.83	13.29	41.29	11.7
Avahi	7.19	6.57	7.83	6.55	14.1	9.78
Propithecus	10.61	8.39	11.48	8.98	20.47	12.47
Palaeopropithecidae	18.12	11.56	19	13.37	30.69	14.57
Lepilemuridae	16.06	8.94	16.45	8.1	26.33	10.43
Cheirogaleidae	29.91	13.06	30.85	13.64	44.05	11.88
Cheirogaleus	17.29	11.35	18.16	11.21	29.33	12.64
Microcebus	8.23	5.73	9.11	5.93	15.03	8.25

APPENDIX II

Supplementary information to accompany Chapter Three Increasing speciation, decreasing trait diversification

Evaluating the effects of missing taxa on estimates of lineage diversification and phenotypic evolutionary rates:

To evaluate the effects of under-sampling species for estimating speciation and phenotypic diversification dynamics, I simulated trees and trait data under constant-rate lineage-invariant models, as well as simulating missing tips on the observed tree to test for rate shifts. The simulations of constant-rate lineage-invariant speciation and trait evolution were used to test the hypothesis of a rate shift when in fact there was none. The simulations of missing tips on the observed tree were used to test for evidence of a rate shift based on the complete sample and compare to the results obtained for the incomplete sample. In other words, are shifts observed with the full tree that are not observed with the incomplete sampled tree?

Test 1: Simulate a single rate Brownian motion trait on the observed phylogeny and test for a rate shift. With the observed tree, I simulated 1000 Brownian motion traits with sigma squared = 0.03 and bounds set based on the range of body sizes in the observed data. I tested for shifts in the BM traits simulated on the simulated full trees using the *brownie.lite* function in phytools. The fit of the data to a single BM rate model and a two-rate model in which the lorisiforms and lemurs were specified to have different rates was compared using likelihood ratio tests. The same test was run on the empirical tree and body mass data, and no BM rate shift was detected (likelihood ratio test of one-rate model to two-rate model, $p=0.17$). No simulated traits rejected the single rates model, suggesting that the tree structure does not result in falsely inferring a rate shift when there was none.

Test 2: Simulate missing tips on the phylogeny, simulate single rate traits on those simulated phylogenies, and test for shifts in lineage and phenotypic diversification. I first simulated the missing tips onto the lorisiform and lemur tree separately and bound the trees for a total of 100 simulated full trees. I then ran the MEDUSA model (Alfaro et al. 2009) on these simulated trees as well as the empirical tree with the genus-level species richness specified. MEDUSA results suggest no shifts in diversification. Of the simulated trees, 52% were inferred to have two rates, and 48% had three rates. These results suggest that MEDUSA infers no rate shifts on the empirical tree, while more shifts were inferred with trees simulated to have the full species richness.

I tested for shifts in the BM traits simulated on the simulated full trees using the *brownie.lite* function in phytools as above. In the simulated datasets, 7% showed significant support for the two-rate model ($p<0.05$), suggesting that a single rate trait evolved on the full tree does not result in falsely inferring a rate shift.

Test 3. Simulate constant rate full trees, randomly prune tips to empirical tree size, estimate the null gamma statistic compared to the observed gamma (Monte Carlo constant rate, MCCR test). I addressed the issue of missing taxa biasing lineage diversification estimates using the constant rate and Monte Carlo constant rate tests in the *laser* package for R. I estimated the gamma statistic for four trees: 1) the MCC tree, 2) the extant and extinct lemur tree, 3) the lorisiform tree, 4) the extant-only lemur tree. One thousand pure birth constant rate trees were simulated to have the true total species richness (MCC: 145 taxa, lemur: 117, lorisiform: 28, extant-only lemurs=100) and randomly pruning the number of missing taxa (MCC: 33, lemur: 16, lorisiform: 11, extant-only lemurs=13). The distribution of gamma values for the simulated trees serve as a null distribution for the observed gamma values [1] and the significant departure from the null model of the observed gamma statistic can be assessed. The gamma statistic for the MCC tree was significantly positively greater than expected for a constant rate model (gamma = 1.93, p = 0.01, SF 5). The overall signal in the MCC tree was evidently driven by the lemur clade, which was significantly positively greater than the constant rate null model (gamma = 1.74, p = 0.02, SF 5), while the lorisiform tree did not differ from a constant rate model (gamma = -0.98, p = 0.43, SF 5). The extant-only lemur tree also had a significantly positive gamma statistic (gamma = 1.99, p = 0.01). These results support the observations of the constant diversification rates through time for the lorisiforms and increasing diversification rates for lemurs.

Test 4. Simulate full trees and BM traits, randomly prune tips to empirical size, and estimate trait evolutionary rate. To evaluate the effect of missing taxa on estimates of phenotypic evolutionary rates, I simulated a pure birth tree with 28 tips (total species richness of lorisiforms) and simulated 1000 continuous traits under a Brownian Motion model with the following conditions: sigma squared = 0.03, from the Brownian Motion model of body mass evolution on the whole strepsirrhine tree, trait lower bound slightly below the lowest (natural log transformed) body mass of lorisiforms, ~50g (3.91), and upper bound larger than the body mass of the largest lorisiforms, *Otolemur crassicaudatus*, ~2000g (ln transform=7.60, fastBM function in phytools). I estimated the sigma squared values for the simulated datasets under a Brownian Motion model (fitContinuous function in Geiger) for the full tree and simulated traits, as well as trees and trait datasets randomly pruned of 17 tips to mimic the missing data for the lorisiform tree. Estimates of sigma squared values for the full and subsampled datasets were close to the true value and did not differ significantly from each other ($\text{mean}_{\text{full}}$=0.0297, 95% confidence intervals, CI, =0.0295-0.030, $\text{mean}_{\text{subsampled}}$=0.0295, 95% CI = 0.0292-0.0298, Wilcoxon rank sum test, W=514800, p>0.05, SF 6). The estimated rates of body mass evolution for lorisiforms in the BAMM analysis are likely robust to incomplete sampling.

Pybus OG, and Harvey PH. 2000. Testing macro–evolutionary models using incomplete molecular phylogenies. Proceedings of the Royal Society of London Series B: Biological Sciences 267(1459):2267-2272.

<u>Results under alternative phylogenetic hypotheses:</u>

<u>With the alternate placement of *Megaladapis* sister to Lemuridae.</u>

Lineage diversification:

The posterior probability of the models with zero, one, two or three rate shifts is given.

Shift posterior distribution:

0	0.47
1	0.35
2	0.13
3	0.035

Bayes factor matrix. The matrix gives the Bayes factor ratio of models proposing numbers of shifts. The ratio of the model proposing one rate shift to the model with no shifts is less than 3, suggesting no rate shifts is the better model.

N SHIFTS	0	1	2	3	4	5
0	1.00	0.90	1.23	1.92	3.51	4.95
1	1.11	1.00	1.36	2.13	3.89	5.48
2	0.82	0.74	1.00	1.56	2.86	4.03
3	0.52	0.47	0.64	1.00	1.83	2.58
4	0.28	0.26	0.35	0.55	1.00	1.41
5	0.20	0.18	0.25	0.39	0.71	1.00

Phenotypic evolution:

Posterior probability of models for zero, one, two, three, or four rate shifts.

Shift posterior distribution:

0	0.003
1	0.56
2	0.31
3	0.01
4	0.03

Bayes factor matrix. The probability of more of more than zero rate shifts is high (BF > 3), and the probability of more than one rate shift is low (BF < 1).

N shifts	0	1	2	3	4	5
0	1.00	0.00	0.00	0.00	0.01	0.01
1	263.49	1.00	0.95	1.20	1.59	3.22
2	278.19	1.06	1.00	1.27	1.68	3.40
3	219.19	0.83	0.79	1.00	1.32	2.68
4	165.43	0.63	0.59	0.75	1.00	2.02
5	81.70	0.31	0.29	0.37	0.49	1.00
6	76.07	0.29	0.27	0.35	0.46	0.93
7	41.77	0.16	0.15	0.19	0.25	0.51
8	88.59	0.34	0.32	0.40	0.54	1.08

<u>Results with extant-only tree</u>

Lineage diversification:

Posterior probability of zero, one, two or three rate shifts

Posterior shift distribution

0	0.46
1	0.35
2	0.14
3	0.04

Bayes factor ratio matrix. The probability of more than zero shifts is low (BF ratio of >1 shift to 0 shifts < 3).

N shifts	0	1	2	3	4	5	6	7
0	1.00	0.89	1.17	1.87	3.45	5.86	4.82	3.66
1	1.12	1.00	1.32	2.10	3.87	6.58	5.42	4.11

2	0.85	0.76	1.00	1.59	2.94	5.00	4.12	3.12
3	0.54	0.48	0.63	1.00	1.85	3.14	2.58	1.96
4	0.29	0.26	0.34	0.54	1.00	1.70	1.40	1.06
5	0.17	0.15	0.20	0.32	0.59	1.00	0.82	0.62
6	0.21	0.18	0.24	0.39	0.71	1.21	1.00	0.76
7	0.27	0.24	0.32	0.51	0.94	1.60	1.32	1.00

Phenotypic evolution:

Posterior distribution of shift probabilities

0	0.25
1	0.49
2	0.20
3	0.05
4	0.009

Bayes factor matrix. The probability of one rate shift compared to zero shifts is 2.91, close to 3, providing weak evidence for one rate shift.

N shifts	0	1	2	3	4	5	6
0	1.00	0.34	0.42	0.69	1.36	2.49	3.85
1	2.91	1.00	1.23	2.02	3.97	7.25	11.21
2	2.38	0.82	1.00	1.64	3.23	5.91	9.14
3	1.45	0.50	0.61	1.00	1.97	3.60	5.56
4	0.73	0.25	0.31	0.51	1.00	1.83	2.83
5	0.40	0.14	0.17	0.28	0.55	1.00	1.55
6	0.26	0.09	0.11	0.18	0.35	0.65	1.00

Comparison of rates of speciation and extinction under alternate topologies

Topology	**Clade**	**speciation rate**	**5% quantile**	**95% quantile**	**extinction rate**	**5% quantile**	**95% quantile**
MCC tree	Lemurs	0.15	0.11	0.2	0.07	0.02	0.14
	Loris	0.14	0.1	0.2	0.07	0.01	0.21
alternate *Megaladapis*	Lemurs	0.15	0.11	0.19	0.07	0.02	0.13
	Loris	0.14	0.1	0.19	0.07	0.01	0.14
Extant-only	Lemurs	0.16	0.12	0.22	0.09	0.03	0.16
	Loris	0.16	0.11	0.22	0.09	0.02	0.16

Supplemental Figures

Figure 1. Histograms comparing posterior distribution of speciation rate estimates among genera MCC tree.

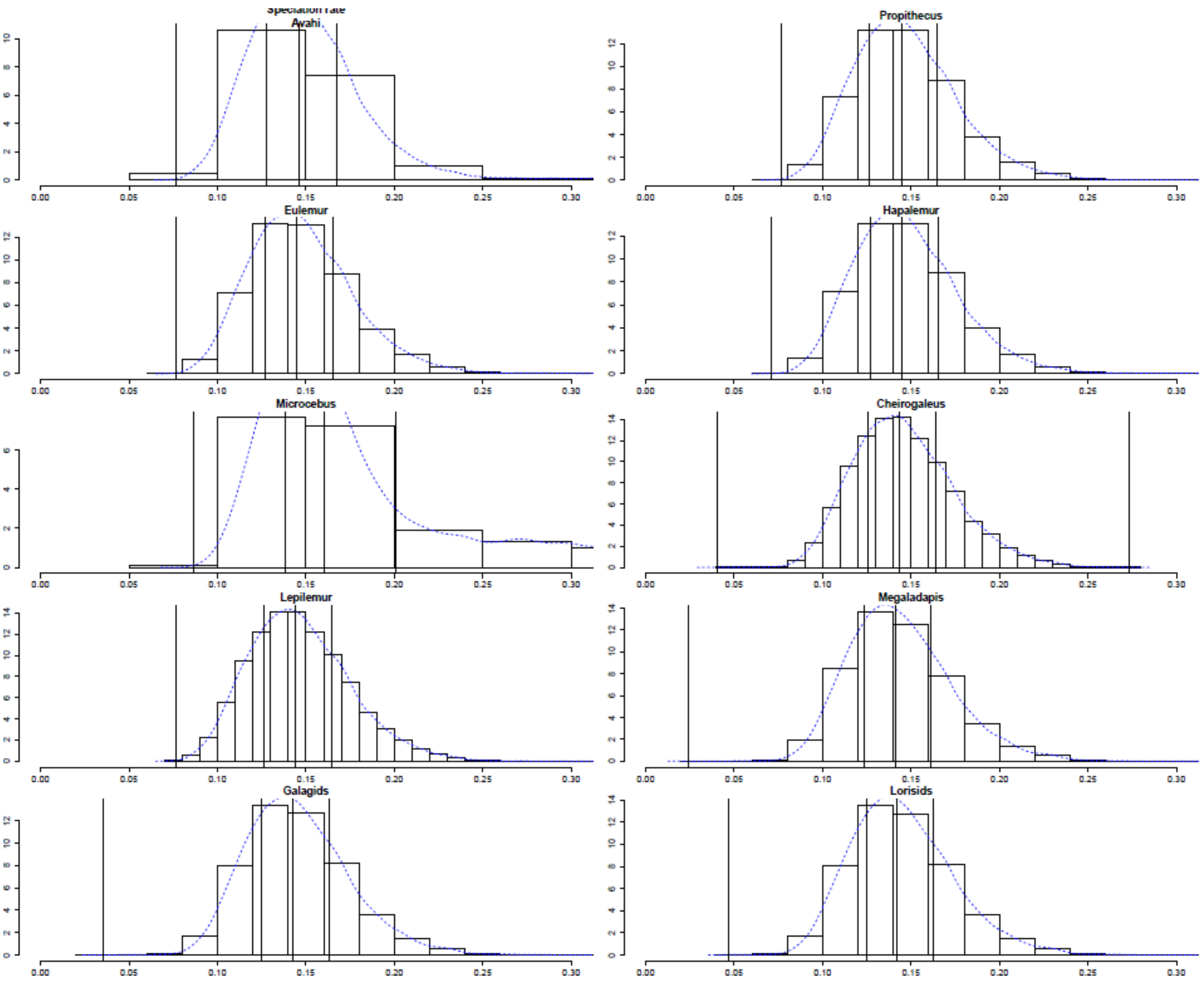

Speciation rate
Avahi
Propithecus
Eulemur
Hapalemur
Microcebus
Cheirogaleus
Lepilemur
Megaladapis
Galagids
Lorisids
0
2
4
6
8
10
12
14
0.00
0.05
0.10
0.15
0.20
0.25
0.30

Figure 2. Histograms comparing null distributions of gamma statistic for the MCC tree (a), the extant and extinct lemurs (b), the lorisiforms (c), and the extant-only lemurs (d). Distributions are from 1000 trees simulated to the total species richness for each tree and randomly pruning the number of taxa missing from the empirical datasets to assess the impact of incomplete sampling on estimates of the tempo of lineage diversification. Grey dashed lines are the quantiles and the grey solid line is the observed gamma statistic. The observed gamma statistic rejects the null hypothesis of constant lineage diversification rate for all trees except lorisiforms. The results corroborate those observed in the BAMM analysis.

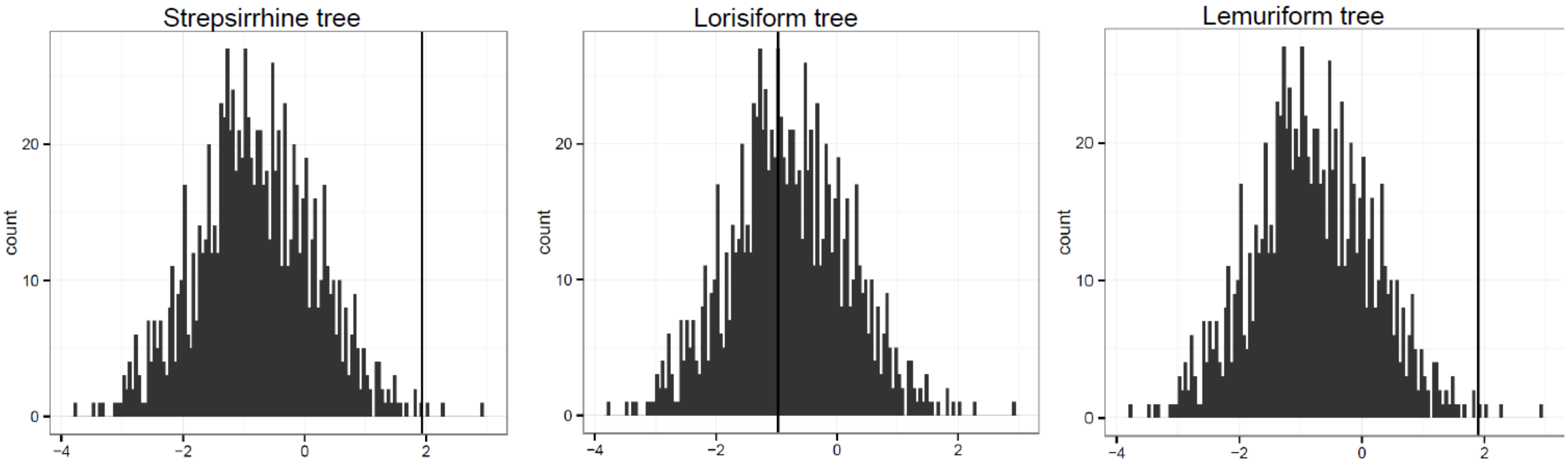


Figure 3. Histograms comparing the estimated Brownian Motion evolutionary rate parameter (sigma squared) for traits simulated to mimic the incomplete sampling of the lorisiform clade. The blue distribution is sigma squared values estimated from the full phylogeny (28 tips), and pink distribution is sigma squared values estimated from the randomly subsampled phylogeny (11 tips). Both distributions are significantly lower than the true value (0.03, black vertical line), and the estimates from the subsampled phylogeny are significantly lower than those from the full phylogeny, according to t-tests.

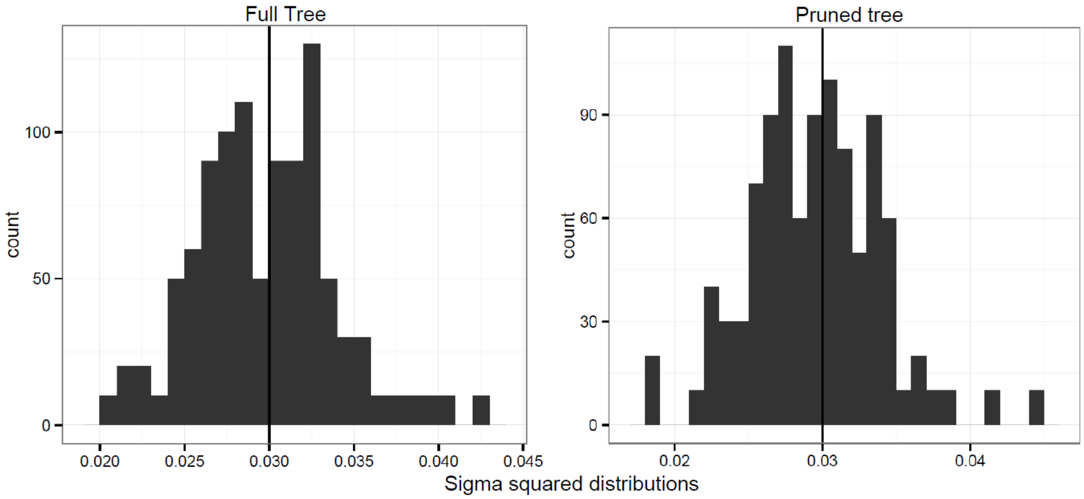
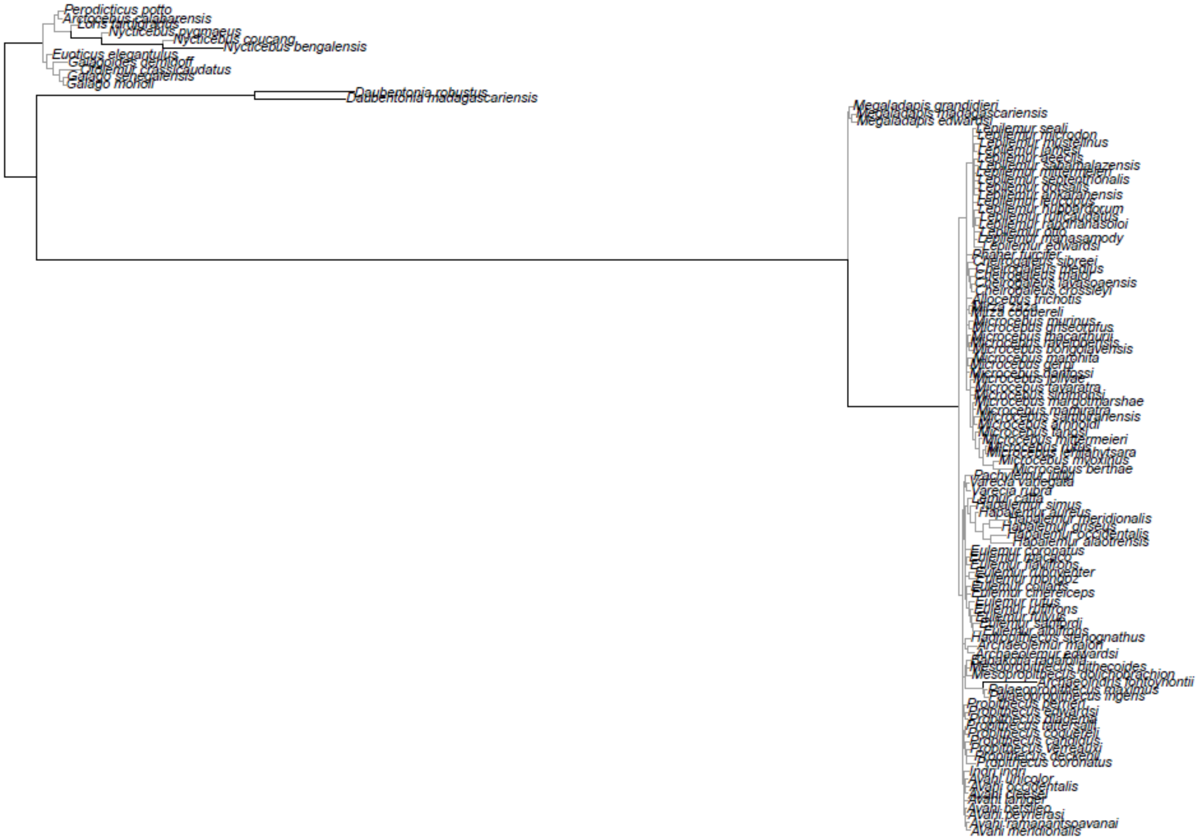


Figure 4. Phylogenetic tree with branch lengths rescaled to the Bayes factor ratio value of the posterior probability of a phenotypic evolutionary rate shift compared to the prior probability of no shift. Black branches have Bayes factor ratios greater than 5, indicating strong support for a shift on that branch, while grey branches had Bayes factor ratios less than 5, indicating low support for a shift. The strongest evidence for a shift is on the branch after the divergence of *Daubentonia* from other lemurs.



Supplemental data. Body mass and niche data. Species without specific studies of diet or activity were assumed to be the same as their congenerics, and given the course grain of the niche categories it should be reliable. For example, all *Avahi* are assumed to be nocturnal folivores.

binomial	**activity**	**diet**	**Mass grams**	**Mass ref**	**Diet reference**	**Activity ref**
Allocebus trichotis	nocturnal	omnivore	77.50	Biebouw 2009	Biebouw 2009	Donati and Borgognini-Tarli 2006
Archaeoindris fontoynontii	diurnal	folivore	161200.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Archaeolemur edwardsi	diurnal	frugivore	26500.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Archaeolemur majori	diurnal	frugivore	18200.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Avahi betsileo	nocturnal	folivore	1050.00	Andriantompohavana et al. 2007	Andriantompohavana et al. 2007	
Avahi cleesei	nocturnal	folivore	1160.66	Thalman and Geissmann 2005; Zaramody et al. 2006	Mittermeier et al. 2010	Donati and Borgognini-Tarli 2006
Avahi laniger	nocturnal	folivore	1161.65	Zaramody et al. 2006	Harcourt 1991; Faulkner and Lehman 2006; Ganzhorn 1985	Donati and Borgognini-Tarli 2006
Avahi meridionalis	nocturnal	folivore	806.73	Zaramody et al. 2007	Norscia et al. 2012	Donati and Borgognini-Tarli 2006
Avahi mooreorum	nocturnal	folivore	924.00	Andriantompohavana et al. 2007		
Avahi occidentalis	nocturnal	folivore	1038.07	Thalman and Geissmann 2000	Thalmann 2001	Donati and Borgognini-Tarli 2006
Avahi peyrierasi	nocturnal	folivore	993.50	Andriantompohavana et al. 2007	Andriantompohavana et al. 2007	

Avahi ramanantsoavanai	nocturnal	folivore	1050.00	Zaramody et al. 2007		Donati and Borgognini-Tarli 2006
Avahi unicolor	nocturnal	folivore	840.00	Andriantompohavana et al. 2007		
Babakotia radafolia	diurnal	folivore	20700.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Cheirogaleus crossleyi	nocturnal	omnivore	395.45	Blanco et al. 2009; this study	Wright and Martin 1995	Donati and Borgognini-Tarli 2006
Cheirogaleus lavasoaensis	nocturnal	omnivore	297.00	Thiele et al. 2013	Thiele et al. 2013	Thiele et al. 2013
Cheirogaleus major	nocturnal	omnivore	317.00	Fietz, 2003		Donati and Borgognini-Tarli 2006
Cheirogaleus medius	nocturnal	omnivore	241.17	Fietz and Ganzhorn 1999	Fietz 2003	Donati and Borgognini-Tarli 2006
Cheirogaleus sibreei	nocturnal	omnivore	243.94	Blanco et al. 2009; this study	pers. Obs. JPH	Donati and Borgognini-Tarli 2006
Daubentonia madagascariensis	nocturnal	omnivore	2675.00	Sterling 1993	Sterling 1994	Donati and Borgognini-Tarli 2006
Daubentonia robustus		omnivore	14200.00	Jungers et al. 2008	Godfrey et al. 2004	Donati and Borgognini-Tarli 2006
Eulemur albifrons	cathemeral	frugivore	2310.00	Junge et al. 2009		Curtis 2006
Eulemur cinereiceps	cathemeral	frugivore	2250.00	Johnson et al. 2005; Mittermeier et al. 2010	Johnson et al. 2005; Mittermeier et al. 2010	Donati and Borgognini-Tarli 2006

Eulemur collaris	cathemeral	frugivore	2180.00	Donati et al., 2007		Donati and Borgognini-Tarli 2006
Eulemur coronatus	cathemeral	frugivore	1200.00	Terranova and Coffman, 1997		Donati and Borgognini-Tarli 2006
Eulemur flavifrons	cathemeral	frugivore	1900.00	Terranova and Coffman, 1997		Schwitzer et al. 2007
Eulemur fulvus	cathemeral	frugivore	1820.00	Rassmussen 1999		Donati and Borgognini-Tarli 2006
Eulemur macaco	cathemeral	frugivore	1820.00	Colquhoun 1997		Donati and Borgognini-Tarli 2006
Eulemur mongoz	cathemeral	frugivore	1043.00	Rasmussen 1999		Donati and Borgognini-Tarli 2006
Eulemur rubriventer	cathemeral	frugivore	2013.50	Glander et al. 1992		Donati and Borgognini-Tarli 2006
Eulemur rufifrons	cathemeral	frugivore	2188.84	Glander et al. 1992		Donati and Borgognini-Tarli 2006
Eulemur rufus	cathemeral	frugivore	1828.98	Junge et al. 2005		Donati and Borgognini-Tarli 2006
Eulemur sanfordi	cathemeral	frugivore	1850.00	Terranova and Coffman, 1997		Donati and Borgognini-Tarli 2006
Hadropithecus stenognathus	diurnal	omnivore	35400.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Hapalemur alaotrensis	diurnal	folivore	1530.41	Mittermeier et al., 2010		Mutschler et al. 1998

Hapalemur aureus	diurnal	folivore	1548.00	Glander et al. 1992		Tan 2000
Hapalemur griseus	diurnal	folivore	935.00	Glander et al. 1992		Tan 2000
Hapalemur meridionalis	diurnal	folivore	855.00	Mittermeier et al., 2010		Tan 2006
Hapalemur occidentalis	diurnal	folivore	900.00	Mittermeier et al., 2010		Tan 2006
Hapalemur simus	diurnal	folivore	2450.00	Tan 1999		Tan 2000
Indri indri	diurnal	folivore	6500.00	Glander and Powzyk 1998		Donati and Borgognini-Tarli 2006
Lemur catta	diurnal	frugivore	2245.00	Koyama 2008		Donati et al. 2013
Lepilemur aeeclis	nocturnal	folivore	988.64	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur ahmansonorum	nocturnal	folivore	610.00	Louis et al. 2006		
Lepilemur ankaranensis	nocturnal	folivore	608.01	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur betsileo	nocturnal	folivore	1150.00	Louis et al. 2006		
Lepilemur dorsalis	nocturnal	folivore	1087.50	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur edwardsi	nocturnal	folivore	978.75	Louis et al. 2006	Thalmann 2001	Donati and Borgognini-Tarli 2006
Lepilemur fleuretae	nocturnal	folivore	980.00	Louis et al. 2006		
Lepilemur grewcockorum	nocturnal	folivore	780.00	Louis et al. 2006		
Lepilemur hollandorum	nocturnal	folivore	1000.00	Louis et al. 2006		

Lepilemur hubbardorum	nocturnal	folivore	771.14	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur jamesorum	nocturnal	folivore	780.00	Louis et al. 2006		
Lepilemur leucopus	nocturnal	folivore	771.14	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur microdon	nocturnal	folivore	721.71	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur milanoii	nocturnal	folivore	720.00	Louis et al. 2006		
Lepilemur mittermeieri	nocturnal	folivore	988.64	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur mustelinus	nocturnal	folivore	852.70	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur otto	nocturnal	folivore	779.05	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur petteri	nocturnal	folivore	630.00	Louis et al. 2006		
Lepilemur randrianasoloi	nocturnal	folivore	920.00	Louis et al. 2006		
Lepilemur ruficaudatus	nocturnal	folivore	692.05	Louis et al. 2006	Ganzhorn 2002	Donati and Borgognini-Tarli 2006
Lepilemur sahamalazensis	nocturnal	folivore	741.48	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur scottorum	nocturnal	folivore	876.00	Louis et al. 2006		

Lepilemur seali	nocturnal	folivore	961.00	Lei et al. 2007		
Lepilemur septentrionalis	nocturnal	folivore	580.00	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur tymerlachsoni	nocturnal	folivore	875.00	Louis et al. 2006		
Lepilemur wrightae	nocturnal	folivore	1150.00	Louis et al. 2006		
Megaladapis edwardsi	diurnal	folivore	85100.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2010
Megaladapis grandidieri	diurnal	folivore	74300.00	Jungers et al. 2008	Godfrey et al. 2004	Godfrey et al. 2010
Megaladapis madagascariensis	diurnal	folivore	46500.00	Jungers et al. 2008	Godfrey et al. 2004	Godfrey et al. 2010
Mesopropithecus dolichobrachion	diurnal	folivore	13700.00	Jungers et al. 2009	Godfrey et al. 2012	Godfrey et al. 2010
Mesopropithecus pithecoides	diurnal	folivore	11300.00	Jungers et al. 2010	Godfrey et al. 2012	Godfrey et al. 2010
Microcebus arnholdi	nocturnal	omnivore	50.00	Louis et al. 2008		Donati and Borgognini-Tarli 2006
Microcebus berthae	nocturnal	omnivore	30.60	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus bongolavensis	nocturnal	omnivore	55.00	Mittermeier et al., 2010		Donati and Borgognini-Tarli 2006
Microcebus danfossi	nocturnal	omnivore	63.00	Olivieri et al. 2007		Donati and Borgognini-Tarli 2006
Microcebus gerpi	nocturnal	omnivore	70.00	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006

Microcebus griseorufus	nocturnal	omnivore	62.60	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus jollyae	nocturnal	omnivore	61.00	Louis et al. 2006		
Microcebus lehilahytsara	nocturnal	omnivore	39.00	Rasoloarison et al. 2013		Donati and Borgognini-Tarli 2006
Microcebus macarthurii	nocturnal	omnivore	53.70	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006
Microcebus mamiratra	nocturnal	omnivore	57.80	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006
Microcebus margotmarshae	nocturnal	omnivore	41.00	Louis et al. 2008		
Microcebus marohita	nocturnal	omnivore	55.76	Rasoloarison et al. 2013		Donati and Borgognini-Tarli 2006
Microcebus mittermeieri	nocturnal	omnivore	59.32	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus murinus	nocturnal	omnivore	48.44	Schmid and Kappeler 1998		Donati and Borgognini-Tarli 2006
Microcebus myoxinus	nocturnal	omnivore	58.33	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus ravelobensis	nocturnal	omnivore	42.51	Randrianambinina et al. 2003		Donati and Borgognini-Tarli 2006

Microcebus rufus	nocturnal	omnivore	43.60	Louis et al. 2006	Atsalis 2007	Donati and Borgognini-Tarli 2006
Microcebus sambiranensis	nocturnal	omnivore	59.91	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus simmonsi	nocturnal	omnivore	50.91	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus tavaratra	nocturnal	omnivore	61.10	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Mirza coquereli	nocturnal	omnivore	289.67	Ganzhorn and Kappeler 1996	Ganzhorn and Kappeler 1996	Donati and Borgognini-Tarli 2006
Mirza zaza	nocturnal	omnivore	300.00	Kappeler et al. 2005		Donati and Borgognini-Tarli 2006
Pachylemur jullyi	diurnal	frugivore	11500.00	Godfrey et al. 2010	Godfrey et al. 2010	Godfrey et al. 2010
Palaeopropithecus ingens	diurnal	folivore	41500.00	Jungers et al. 2008	Godfrey et al. 2010	Godfrey et al. 2010
Palaeopropithecus maximus	diurnal	folivore	45800.00	Jungers et al. 2008	Godfrey et al. 2010	Godfrey et al. 2010
Phaner electromontis	nocturnal	omnivore	387.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010
Phaner furcifer	nocturnal	omnivore	450.00	Ganzhorn and Kappeler 1996	Ganzhorn and Kappeler 1996	Donati and Borgognini-Tarli 2006
Phaner pallescens	nocturnal	omnivore	327.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010
Phaner parienti	nocturnal	omnivore	360.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010

Propithecus candidus	diurnal	folivore	5500.00	Lehman et al. 2005	Lehman et al. 2005	Donati and Borgognini-Tarli 2006
Propithecus coquereli	diurnal	folivore	3700.00	Kappeler 1991		Donati and Borgognini-Tarli 2006
Propithecus coronatus	diurnal	folivore	3900.00	Mittermeier et al., 2010		Donati and Borgognini-Tarli 2006
Propithecus deckenii	diurnal	folivore	2810.00	Junge et al. 2005		Donati and Borgognini-Tarli 2006
Propithecus diadema	diurnal	folivore	5190.00	Irwin 2006	Irwin 2006	Donati and Borgognini-Tarli 2006
Propithecus edwardsi	diurnal	folivore	5742.50	Glander et al. 1992	Hemingway 1998	Donati and Borgognini-Tarli 2006
Propithecus perrieri	diurnal	folivore	4332.50	Lehman et al. 2005		Donati and Borgognini-Tarli 2006
Propithecus tattersalli	diurnal	folivore	3500.00	Meyers and Wright 1993	Irwin 2007	Donati and Borgognini-Tarli 2006
Propithecus verreauxi	diurnal	folivore	3190.00	Lewis and Kappeler 2005		Donati and Borgognini-Tarli 2006
Varecia rubra	diurnal	frugivore	3470.00	Vasey 2005		Donati and Borgognini-Tarli 2006
Varecia variegata	diurnal	frugivore	3665.00	Baden et al. 2008	Balko and Underwood 2005	Donati and Borgognini-Tarli 2006

Galago moholi	nocturnal	omnivore	200.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Galago senegalensis	nocturnal	omnivore	247.75	Nekaris and Bearder 2011	Nekaris and Bearder 2005	Nekaris and Bearder 2011
Arctocebus calabarensis	nocturnal	omnivore	309.00	Nekaris and Bearder 2011	Nekaris and Bearder 2006	Nekaris and Bearder 2011
Euoticus elegantulus	nocturnal	omnivore	274.00	Nekaris and Bearder 2011	Nekaris and Bearder 2007	Nekaris and Bearder 2011
Galagoides demidoff	nocturnal	omnivore	61.50	Nekaris and Bearder 2011	Nekaris and Bearder 2008	Nekaris and Bearder 2011
Otolemur crassicaudatus	nocturnal	omnivore	1150.00	Nekaris and Bearder 2011	Nekaris and Bearder 2009	Nekaris and Bearder 2011
Otolemur garnetti	nocturnal	omnivore	764.00	Nekaris and Bearder 2011	Nekaris and Bearder 2010	Nekaris and Bearder 2011
Perodicticus potto	nocturnal	omnivore	1000.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Nycticebus coucang	nocturnal	omnivore	652.50	Nekaris and Bearder 2011	Nekaris and Bearder 2012	Nekaris and Bearder 2011
Nycticebus bengalensis	nocturnal	omnivore	1270.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Nycticebus pygmaeus	nocturnal	omnivore	307.00	Nekaris and Bearder 2011	Nekaris and Bearder 2012	Nekaris and Bearder 2011
Nycticebus javanicus	nocturnal	omnivore	700.00	Nekaris et al. 2014	Nekaris et al. 2014	Nekaris et al. 2014
Nycticebus menagensis	nocturnal	omnivore	532.50	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Loris tardigradus	nocturnal	omnivore	229.50	Nekaris and Bearder 2011	Nekaris and Bearder 2012	Nekaris and Bearder 2011
Galago thomasi	nocturnal	omnivore	78.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Galago alleni	nocturnal	omnivore	439.33	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011

Galagoides zanzibaricus	nocturnal	omnivore	149.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Galagoides cocos	nocturnal	omnivore	150.00	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011
Galago matschiei	nocturnal	omnivore	210.50	Nekaris and Bearder 2011	Nekaris and Bearder 2011	Nekaris and Bearder 2011

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APPENDIX III

Supplemental materials to accompany Chapter Four

Supplemental methods

Phylogeny: The phylogeny from Chapter 1 was ~90% complete. The 16 species that were not in the original phylogeny were grafted to it using the *bind.tip* function in the *ape* package (Paradis et al. 2004) in R. Species were added to the phylogeny by bracketing them with congeners in the phylogeny based on original publications (Louis 2006, Lei et al. 2008). Because divergence times were not available for these taxa, they were added to the middle of the internodes of their bracketing species. For *Phaner* species, *P. furcifer* was the only species in the original phylogeny, and three congeners were added to it between 0.5 and 1.5 million years ago (Ma) based on the upper credible interval of divergence time estimates from mitochondrial genomes in an unpublished book chapter (Louis et al. in press). The code for replicating this grafting procedure is included at the end of this supplement.

Event-based parametric biogeographic inference: Time stratified dispersal multipliers: BioGeoBEARS (Matzke 2014) allows the user to include time stratified dispersal multipliers. To replicate the hypothesized timing of biogeographic events, I set up the following time-varying dispersal multipliers.

<u>Ecoregional and river barrier</u>: the distribution of wet, dry and spiny forests most likely took their current geographic positions in the Miocene, and hypothesized riverine barriers most likely formed in the Pliocene (Wells 2003). I set up the following three dispersal multiplier matrices that were stratified from the present to 4.9 Ma, 5 – 15 Ma and 15 - 45 Ma. 15Ma was used for the Miocene because of time binning constraints in BioGeoBEARS.

Pliocene: dispersal among habitat types is low (0.25), dispersal across river barriers is very low (0.0001).

C	NE	SE	NW	SW	
1	0.25	0.25	0.25	0.25	
0.25	1	0.0001	0.0001	0.0001	
0.25	0.0001	1	0	0.25	
0.25	0.00001		0	1	0.0001
0.25	0	0.0001	0.0001	1	

Miocene: Dispersal among habitat types is low (0.25)

C	NE	SE	NW	SW
1	0.25	0.25	0.25	0.25
0.25	1	1	0.25	0
0.25	1	1	0	0.25
0.25	0.25	0	1	1
0.25	0	0.25	1	1

Pre-Miocene: Dispersal is based on adjacency

C	NE	SE	NW	SW
1	1	1	1	1
1	1	1	1	0
1	1	1	0	0.5
1	1	0	1	1

1	0	0.5	1	1

<u>Wathershed refugia, highlands dispersal:</u> This hypothesis suggests dispersal among lowland regions was low and to and from the central highlands was high in the Pleistocene, adjacency based dispersal probabilities before that.

Plesitocene: Dispersal probability to or from the central highlands is high (1), and low among other regions (0.0001-0).

C	NE	SE	NW	SW	
1	1	1	1	1	
1	1	0.0001	0.0001	0.0001	
1	0.0001	1	0	0.0001	
1	0.00001		0	1	0.0001
1	0	0.0001	0.0001	1	

Adjacency-based dispersal multipliers

C	NE	SE	NW	SW
1	1	1	1	1
1	1	1	1	0
1	1	1	0	0.5
1	1	0	1	1
1	0	0.5	1	1

Table 1. Summary of the number and proportion of biogeographic events simulated on the phylogeny under the best biogeographic model with the east *versus* west area bioregion definition using Bayesian stochastic mapping. Founder = founder event speciation, disp = anagenetic dispseral, e = extinction, subset = subset sympatry, vicar = vicariance, symp = exact-range inheritance sympatry

	founder	%	disp	%	e	subset	%	vic	%	symp	%	Total events
means	15.49	11.45	23.31	17.23	0.00	15.01	11.09	5.66	4.18	75.84	56.05	135.30
stdevs	2.83		1.98		0.00	4.04		1.88		3.48		1.98

Table 2. Summary of the number and proportion of biogeographic events simulated on the phylogeny under the best biogeographic model with the north *versus* south area bioregion definition using Bayesian stochastic mapping. Founder = founder event speciation, disp = anagenetic dispseral, e = extinction, subset = subset sympatry, vicar = vicariance, symp = exact-range inheritance sympatry

	founder	%	disp	%	e	subset	%	vicar	%	symp	%	Total events
means	20.45	15.09	23.45	17.31	0.00	14.21	10.49	5.84	4.31	71.50	52.77	135.50
stdevs	3.00		2.42		0.00	3.52		2.36		3.66		2.42

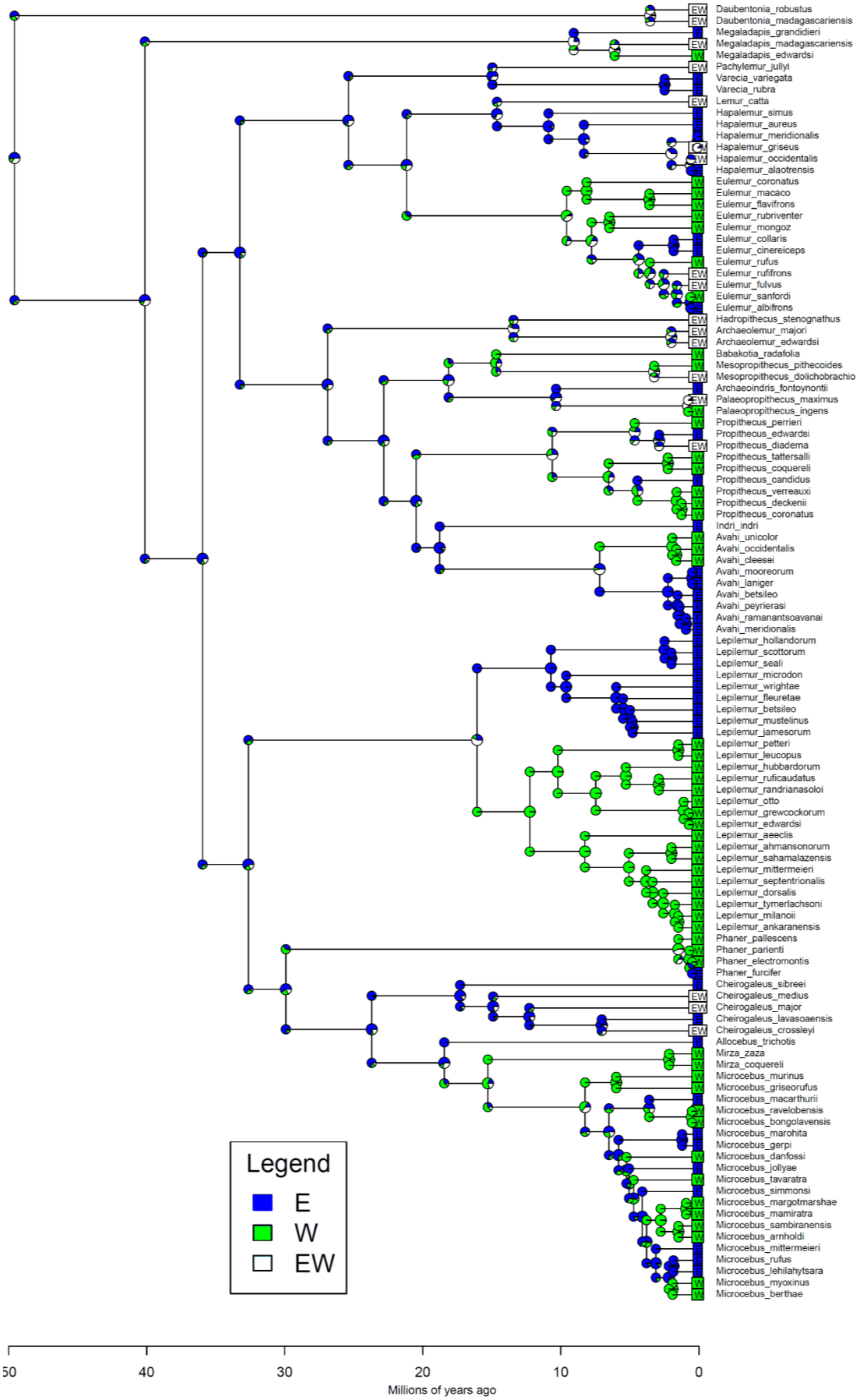
Supplemental code

Adding missing species:

Species topology and divergence times from:
Lei, R. et al. (2008). Special Publications of Texas Tech University 53: 1-48.
Louis, E. E. (2006). Molecular and morphological analyses of the sportive lemurs (Family Megaladapidae: Genus Lepilemur) reveals 11 previously unrecognized species, Museum of Texas Tech University.
Paradis, E. et al. (2004). Bioinformatics 20: 289-290.

```
##start code
tree2<-bind.tip(tree, "Phaner_pallescens",
edge.length=1.5,where=which(tree$tip.label=="Phaner_furcifer"), position=1.5)
tree2<-bind.tip(tree2, "Phaner_electromontis",
edge.length=0.5,where=which(tree$tip.label=="Phaner_furcifer"), position=0.5)
tree2<-bind.tip(tree2, "Phaner_parienti", where=186, edge.length=0.7, position=0.2)
tree2<-bind.tip(tree2, "Lepilemur_ahmansonorum",
where=which(tree$tip.label=="Lepilemur_sahamalazensis"), edge.length=2, position=2)
tree2$edge.length[198]#4.812755
tree2<-bind.tip(tree2, "Lepilemur_betsileo", where=206, edge.length=5, position=0.187245)
tree2<-bind.tip(tree2, "Lepilemur_fleuretae", where=207, edge.length=5.5, position=0.5)
tree2<-bind.tip(tree2, "Lepilemur_wrightae", where=208, edge.length=6, position=0.5)
tree2$edge.length[198]#4.812755
tree2$tip.label[34]<-"Lepilemur_grewcockorum"
tree2<-bind.tip(tree2, "Lepilemur_hollandorum",
where=which(tree$tip.label=="Lepilemur_seali"), edge.length=2.5, position=2.5)
tree2$edge.length[207]
tree2<-bind.tip(tree2, "Lepilemur_scottorum", where=which(tree$tip.label=="Lepilemur_seali"),
edge.length=2, position=2)
tree2<-bind.tip(tree2, "Lepilemur_scottorum", where=which(tree$tip.label=="Lepilemur_seali"),
edge.length=2, position=2)
tree2$edge.length[186]
tree2<-bind.tip(tree2, "Lepilemur_milanoii",
where=which(tree$tip.label=="Lepilemur_ankaranensis"), edge.length=1.5, position=1.5)
tree2<-bind.tip(tree2, "Lepilemur_petteri",
where=which(tree$tip.label=="Lepilemur_leucopus"), edge.length=1.5, position=1.5)
tree2$edge.length[190]
tree2<-bind.tip(tree2, "Lepilemur_tymerlachsoni", where=211, edge.length=1.75, position=0.25)
tree2<-bind.tip(tree2, "Avahi_mooreorum", where=which(tree$tip.label=="Avahi_laniger"),
edge.length=0.5, position=0.5)
tree2$tip.label[46]<-"Lepilemur_jamesorum"
```

Figure 1. Ancestral range inferences from the best-fitting model of historical biogeography with the east *versus* west bioregion definition, from BioGeoBEARS. The best fitting model was the dispersal-extinction-cladogenesis model with the addition of the founder event parameter, and a dispersal probability transition matrix in which the probability of dispersing from east to west (0.5) was higher than *vice versa* (0.25). Color codes correspond to range states (3 possible) as depicted in the legend. The pie charts at nodes represent the proportional likelihood that the ancestral ranges were in each state.


Daubentonia_robustus
Daubentonia_madagascariensis
Megaladapis_grandidieri
Megaladapis_madagascariensis
Megaladapis_edwardsi
Pachylemur_jullyi
Varecia_variegata
Varecia_rubra
Lemur_catta
Hapalemur_simus
Hapalemur_aureus
Hapalemur_meridionalis
Hapalemur_griseus
Hapalemur_occidentalis
Hapalemur_alaotrensis
Eulemur_coronatus
Eulemur_macaco
Eulemur_flavifrons
Eulemur_rubriventer
Eulemur_mongoz
Eulemur_collaris
Eulemur_cinereiceps
Eulemur_rufus
Eulemur_rufifrons
Eulemur_fulvus
Eulemur_sanfordi
Eulemur_albifrons
Hadropithecus_stenognathus
Archaeolemur_majori
Archaeolemur_edwardsi
Babakotia_radofila
Mesopropithecus_pithecoides
Mesopropithecus_dolichobrachio
Archaeoindris_fontoynontii
Palaeopropithecus_maximus
Palaeopropithecus_ingens
Propithecus_perrieri
Propithecus_edwardsi
Propithecus_diadema
Propithecus_tattersalli
Propithecus_coquereli
Propithecus_candidus
Propithecus_verreauxi
Propithecus_deckenii
Propithecus_coronatus
Indri_indri
Avahi_unicolor
Avahi_occidentalis
Avahi_cleesei
Avahi_mooreorum
Avahi_laniger
Avahi_betsileo
Avahi_peyrierasi
Avahi_ramanantsoavanai
Avahi_meridionalis
Lepilemur_hollandorum
Lepilemur_scottorum
Lepilemur_seali
Lepilemur_microdon
Lepilemur_wrightae
Lepilemur_fleuretae
Lepilemur_betsileo
Lepilemur_mustelinus
Lepilemur_jamesorum
Lepilemur_petteri
Lepilemur_leucopus
Lepilemur_hubbardorum
Lepilemur_ruficaudatus
Lepilemur_randrianasoloi
Lepilemur_otto
Lepilemur_grewcockorum
Lepilemur_edwardsi
Lepilemur_aeeclis
Lepilemur_ahmansonorum
Lepilemur_sahamalazensis
Lepilemur_mittermeieri
Lepilemur_septentrionalis
Lepilemur_dorsalis
Lepilemur_tymerlachsoni
Lepilemur_milanoii
Lepilemur_ankaranensis
Phaner_pallescens
Phaner_parienti
Phaner_electromontis
Phaner_furcifer
Cheirogaleus_sibreei
Cheirogaleus_medius
Cheirogaleus_major
Cheirogaleus_lavasoaensis
Cheirogaleus_crossleyi
Allocebus_trichotis
Mirza_zaza
Mirza_coquereli
Microcebus_murinus
Microcebus_griseorufus
Microcebus_macarthurii
Microcebus_ravelobensis
Microcebus_bongolavensis
Microcebus_marohita
Microcebus_gerpi
Microcebus_danfossi
Microcebus_jollyae
Microcebus_tavaratra
Microcebus_simmonsi
Microcebus_margotmarshae
Microcebus_mamiratra
Microcebus_sambiranensis
Microcebus_arnholdi
Microcebus_mittermeieri
Microcebus_rufus
Microcebus_lehilahytsara
Microcebus_myoxinus
Microcebus_berthae
Legend
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EW
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10
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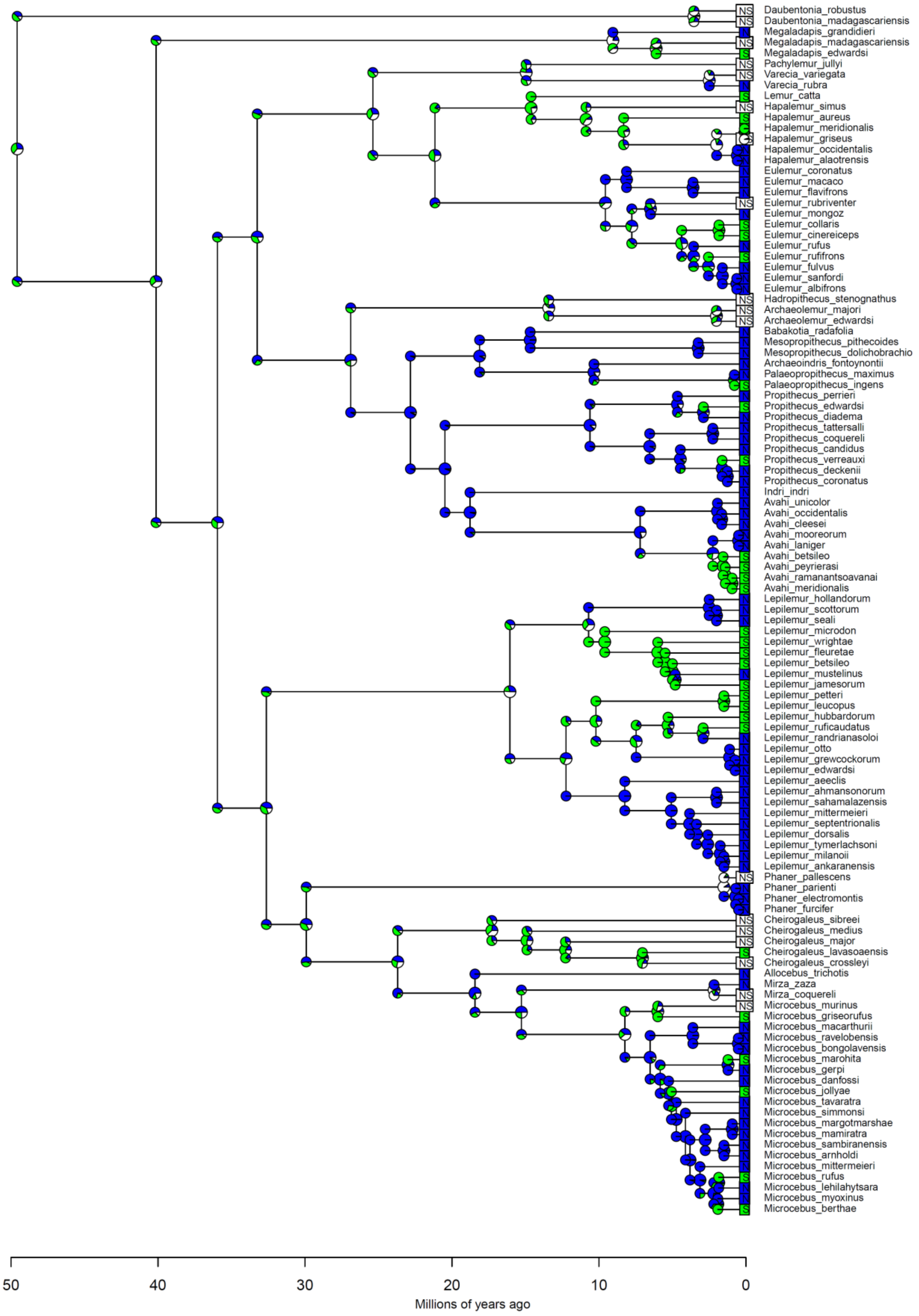
Millions of years ago

Figure 2. Ancestral range inferences from the best-fitting model of historical biogeography with the north *versus* south bioregion definition, from BioGeoBEARS. The best fitting model was the dispersal-extinction-cladogenesis model with the addition of the founder event parameter, and a dispersal probability transition matrix in which the probability of dispersing from south to north (0.5) was higher than *vice versa* (0.25). Color codes correspond to range states (3 possible) as depicted in the legend. The pie charts at nodes represent the proportional likelihood that the ancestral ranges were in each state.


Daubentonia_robustus
Daubentonia_madagascariensis
Megaladapis_grandidieri
Megaladapis_madagascariensis
Megaladapis_edwardsi
Pachylemur_jullyi
Varecia_variegata
Varecia_rubra
Lemur_catta
Hapalemur_simus
Hapalemur_aureus
Hapalemur_meridionalis
Hapalemur_griseus
Hapalemur_occidentalis
Hapalemur_alaotrensis
Eulemur_coronatus
Eulemur_macaco
Eulemur_flavifrons
Eulemur_rubriventer
Eulemur_mongoz
Eulemur_collaris
Eulemur_cinereiceps
Eulemur_rufus
Eulemur_rufifrons
Eulemur_fulvus
Eulemur_sanfordi
Eulemur_albifrons
Hadropithecus_stenognathus
Archaeolemur_majori
Archaeolemur_edwardsi
Babakotia_radafolia
Mesopropithecus_pithecoides
Mesopropithecus_dolichobrachio
Archaeoindris_fontoynontii
Palaeopropithecus_maximus
Palaeopropithecus_ingens
Propithecus_perrieri
Propithecus_edwardsi
Propithecus_diadema
Propithecus_tattersalli
Propithecus_coquereli
Propithecus_candidus
Propithecus_verreauxi
Propithecus_deckenii
Propithecus_coronatus
Indri_indri
Avahi_unicolor
Avahi_occidentalis
Avahi_cleesei
Avahi_mooreorum
Avahi_laniger
Avahi_betsileo
Avahi_peyrierasi
Avahi_ramanantsoavanai
Avahi_meridionalis
Lepilemur_hollandorum
Lepilemur_scottorum
Lepilemur_seali
Lepilemur_microdon
Lepilemur_wrightae
Lepilemur_fleuretae
Lepilemur_betsileo
Lepilemur_mustelinus
Lepilemur_jamesorum
Lepilemur_petteri
Lepilemur_leucopus
Lepilemur_hubbardorum
Lepilemur_ruficaudatus
Lepilemur_randrianasoloi
Lepilemur_otto
Lepilemur_grewcockorum
Lepilemur_edwardsi
Lepilemur_aeeclis
Lepilemur_ahmansonorum
Lepilemur_sahamalazensis
Lepilemur_mittermeieri
Lepilemur_septentrionalis
Lepilemur_dorsalis
Lepilemur_tymerlachsoni
Lepilemur_milanoii
Lepilemur_ankaranensis
Phaner_pallescens
Phaner_parienti
Phaner_electromontis
Phaner_furcifer
Cheirogaleus_sibreei
Cheirogaleus_medius
Cheirogaleus_major
Cheirogaleus_lavasoaensis
Cheirogaleus_crossleyi
Allocebus_trichotis
Mirza_zaza
Mirza_coquereli
Microcebus_murinus
Microcebus_griseorufus
Microcebus_macarthurii
Microcebus_ravelobensis
Microcebus_bongolavensis
Microcebus_marohita
Microcebus_gerpi
Microcebus_danfossi
Microcebus_jollyae
Microcebus_tavaratra
Microcebus_simmonsi
Microcebus_margotmarshae
Microcebus_mamiratra
Microcebus_sambiranensis
Microcebus_arnholdi
Microcebus_mittermeieri
Microcebus_rufus
Microcebus_lehilahytsara
Microcebus_myoxinus
Microcebus_berthae
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Millions of years ago

APPENDIX IV

Supplemental materials to accompany Chapter Five

Supplemental methods

Phylogeny: The phylogeny from Chapter 1 was ~90% complete. The 16 species that were not in the original phylogeny were grafted to it using the *bind.tip* function in the *ape* package (Paradis et al. 2004) in R. Species were added to the phylogeny by bracketing them with congeners in the phylogeny based on original publications (Lei et al. 2008; Louis 2006). Because divergence times were not available for these taxa, they were added to the middle of the internodes of their bracketing species. For *Phaner* species, *P. furcifer* was the only species in the original phylogeny, and three congeners were added to it between 0.5 and 1.5 million years ago (Ma) based on the upper credible interval of divergence time estimates from mitochondrial genomes in an unpublished book chapter (Louis et al. in press). The code for replicating this grafting procedure is included at the end of this supplement.

Traits: I collected data on the following traits from the literature: 1) body size (ln g), 2) diet category (omnivore, folivore, frugivore), 3) activity pattern (diurnal, nocturnal, cathemeral, SDF 4). Detailed natural history data were not available for many newly described species, especially in the genera *Lepilemur, Microcebus, Avahi*, and data for those taxa were taken from Mittermeier et al. 2013 and generalizing from well-studied congeners assumed to have similar niches; e.g., the genera mentioned were all assumed to be nocturnal, all *Lepilemur* and *Avahi* were assumed to be folivores, *Microcebus* assumed to be omnivores. These generalizations should apply based on available knowledge.

Spatial autocorrelation: I included spatial correlation matrices in the error structure of the linear mixed models (lmms) using the correlation arguments of the *lme* function (*nlme* package in R). I compared the fit of models of each dependent variable against the intercept (e.g., MNTD ~ 1) with and without the following spatial autocorrelation decay matrix types: Gaussian (corGaus), spherical (corSpher), linear (corLin), and ratio (corRatio). For all variables and in the downstream lmms, including a ratio spatial decay matrix was the best model fit.

Phylogenetic beta diversity: I calculated pairwise site dissimilarities for taxonomy using the Sorenson's index (*vegdist* function in vegan), the phylogenetic Sorenson's index (*phylosor* function in picante), and the functional community dissimilarity. Functional dissimilarity was calculated by first converting the species traits (diet, activity pattern and ln mass) to a Gower dissimilarity matrix (*daisy* function in cluster), clustering species based on their dissimilarities using an unweighted pair group method with arithmetic mean (UPGMA) algorithm (*upgma* function in phangorn), and calculating the pairwise site dissimilarities with the phylogenetic community dissimilarity algorithm, with the functional trait UPGMA as the tree (*pcd* function in picante). I conducted multiple Mantel correlations of phylogenetic, taxonomic, and functional beta diversity, and extracted the residual of the following dissimilarities: residual phylogenetic beta controlling for taxonomic beta (Mantel correlation coefficient = 0.56, $p<0.001$), and residual functional beta controlling for phylogenetic beta (Mantel $r=0.52$, $p<0.001$). I then conducted multiple Mantel correlations of elevation, climate, annual precipitation, altitude, plant productivity (NDVI) dissimilarity matrices, and geographic distance with residual phylogenetic and functional beta diversity. Each environmental predictor dissimilarity matrix was based on Euclidean distances of the z-scores of natural log transformed WorldClim/NDVI data, and the climate matrix was based on the Euclidean distance matrix of the z-scores of the following of natural log variables: mean temperature, isothermality, standard deviation in temperature, annual precipitation, coefficient of variation of annual precipitation. The geographic distance matrices were calculated based on the distances among centroids of PAs using the *earth.dist* function in the *fossil* package.

Supplemental results:

Phylogenetic beta diversity: Residual phylo-beta diversity was correlated with elevation dissimilarity (r=0.13, p<0.01), precipitation dissimilarity (r=0.03, p < 0.01) and geographic distance (r=-0.02, p=0.001). In multiple Mantel tests that included NDVI dissimilarity, only NDVI was significant (multiple r=0.03, p < 0.01). The climate dissimilarity from multiple climate variables was not significant (multiple Mantel r=0.004, p >0.05), nor was the precipitation dissimilarity (r=-0.006, p>0.05).

Supplemental tables

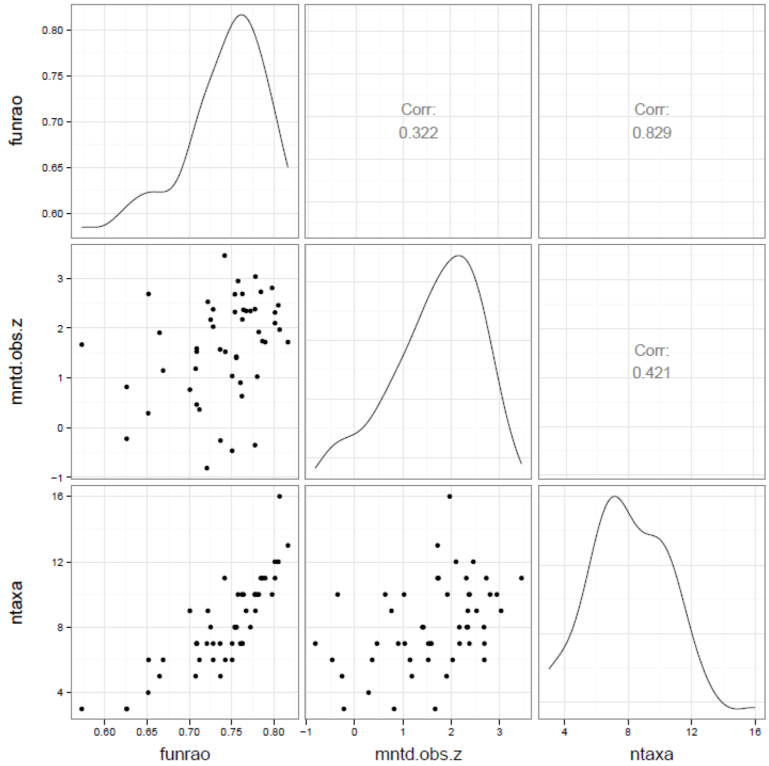
Table 1. Local community MNTD. Cells in bold are significantly overdispersed.

PA	Species richness	MNTD	P
Ambatovaky	**12**	**2.10**	**0.99**
Ambohitantely	3	-0.22	0.37
AnadabolavaBetsimalaho	7	-0.81	0.22
Analamaintso	**11**	**2.31**	**0.99**
Analamazoatra	**11**	**1.72**	**0.96**
Analamerana	9	3.03	1.00
Andohahela1	**8**	**2.17**	**0.99**
Andohahela2	7	1.59	0.94
Anjanaharibe.Sud	10	1.02	0.84
Anjozorobe	**10**	**2.37**	**0.99**
Ankarafantsika	10	-0.35	0.37
Ankarana	**8**	**2.32**	**0.98**
BaiedeBaly	**5**	**1.90**	**0.98**
Bemarivo	7	1.57	0.94
Berenty	7	1.53	0.94
Betampona	**10**	**1.92**	**0.98**
Beza.Mahafaly	6	0.36	0.65
Bora	**6**	**2.03**	**0.97**
CapSt.Marie	3	0.82	0.85
CAZ	**16**	**1.97**	**0.98**
Central Menabe.Kirindy	9	0.76	0.77
COFAV N	**12**	**2.46**	**0.99**
COFAV S	**13**	**1.72**	**0.95**
Daraina	**8**	**2.68**	**0.99**
Fandriana	**10**	**2.80**	**1.00**
Isalo	7	0.90	0.81
Kalambatritra	**7**	**2.17**	**0.98**

Katsijy	6	-0.46	0.35
Kianjavato	6	1.52	0.94
Kirindy.Mitea	8	1.40	0.91
LacAlaotra	**3**	**1.67**	**0.99**
Makira	**11**	**1.74**	**0.97**
Mananara	**11**	**2.73**	**1.00**
Maningoza	7	1.04	0.85
Manombo	**7**	**2.69**	**1.00**
Manongarivo	**9**	**2.34**	**0.99**
Marojejy	10	0.63	0.73
Maromandia	5	-0.26	0.40
Masoala	**10**	**2.94**	**1.00**
Midongy	**7**	**2.37**	**1.00**
Mitsinjo	**10**	**2.38**	**0.99**
Mt.dAmbreNP	6	1.15	0.88
Mt.dAmbreSR	**6**	**2.68**	**0.99**
NosyLokobe	4	0.29	0.64
Onilahy	7	0.46	0.66
Tsaratanana	**8**	**2.34**	**0.99**
Tsimanampetsotsa	5	1.18	0.89
TsingydeBemeraha	**11**	**3.45**	**1.00**
TsingydeNamaroka	**9**	**2.53**	**0.99**
Zombitse	8	1.42	0.92

Supplemental figures legends

SF 1. Pair-wise correlations among alpha community structure variables. Funrao: functional diversity as measured by Rao’s quadratic entropy. Mntd.obs.z: standardized effect size of mean nearest taxon distance. Ntaxa: number of species.



SF 2. Residual phylogenetic beta diversity predicted by NDVI. The slope represents the significant Mantel correlation coefficient.

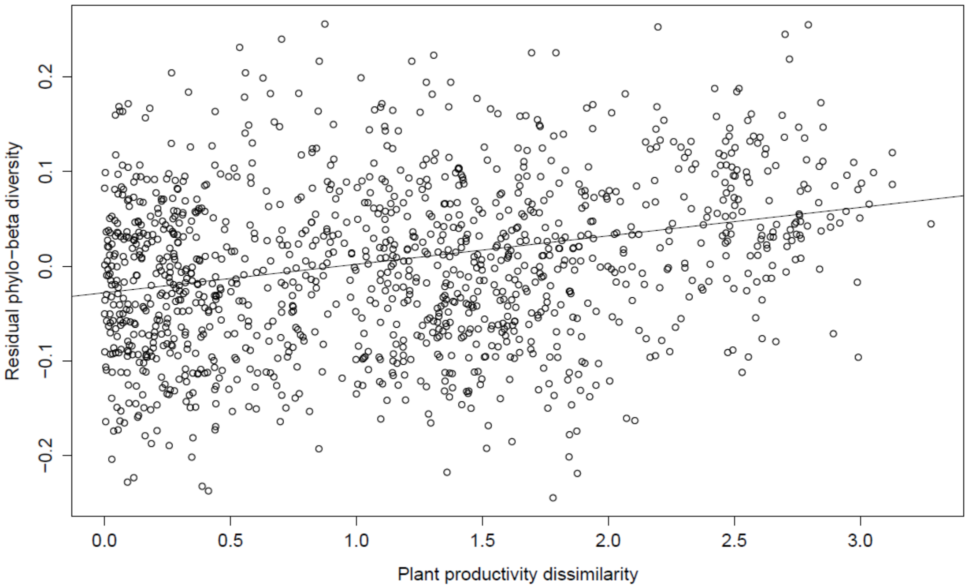


Table 2. Trait data table with references

Binomial name	**Activity**	**Diet**	**Mass (g)**	**Mass ref**	**Diet ref**	**Activity ref**
Allocebus trichotis	nocturnal	omnivore	77.50	Biebouw 2009	Biebouw 2009	Donati and Borgognini-Tarli 2006
Archaeoindris fontoynontii	diurnal	folivore	161200.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Archaeolemur edwardsi	diurnal	frugivore	26500.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Archaeolemur majori	diurnal	frugivore	18200.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Avahi betsileo	nocturnal	folivore	1050.00	Andriantompohavana et al. 2007	Andriantompohavana et al. 2007	
Avahi cleesei	nocturnal	folivore	1160.66	Thalman and Geissmann 2005; Zaramody et al. 2006	Mittermeier et al. 2010	Donati and Borgognini-Tarli 2006
Avahi laniger	nocturnal	folivore	1161.65	Zaramody et al. 2006	Harcourt 1991; Faulkner and Lehman 2006; Ganzhorn 1985	Donati and Borgognini-Tarli 2006
Avahi meridionalis	nocturnal	folivore	806.73	Zaramody et al. 2007	Norscia et al. 2012	Donati and Borgognini-Tarli 2006
Avahi mooreorum	nocturnal	folivore	924.00	Andriantompohavana		
Avahi occidentalis	nocturnal	folivore	1038.07	Thalman and Geissmann 2000	Thalmann 2001	Donati and Borgognini-Tarli 2006
Avahi peyrierasi	nocturnal	folivore	993.50	Andriantompohavana et al. 2007	Andriantompohavana et al. 2007	

Avahi ramanantsoavanai	nocturnal	folivore	20464.79	Zaramody et al. 2007		Donati and Borgognini-Tarli 2006
Avahi unicolor	nocturnal	folivore	840.00	Andriantompohavana et al. 2007		
Babakotia radafolia	diurnal	folivore	20700.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Cheirogaleus crossleyi	nocturnal	omnivore	395.45	Blanco et al. 2009; this study	Wright and Martin 1999	Donati and Borgognini-Tarli 2006
Cheirogaleus lavasoaensis	nocturnal	omnivore	297.00	Thiele et al. 2013	Thiele et al. 2013	Thiele et al. 2013
Cheirogaleus major	nocturnal	omnivore	137.91	Fietz, 2003		Donati and Borgognini-Tarli 2006
Cheirogaleus medius	nocturnal	omnivore	241.17	Fietz and Ganzhorn 1999	Fietz 2003	Donati and Borgognini-Tarli 2006
Cheirogaleus sibreei	nocturnal	omnivore	243.94	Blanco et al. 2009; this study	pers. Obs. JPH	Donati and Borgognini-Tarli 2006
Daubentonia madagascariensis	nocturnal	omnivore	2675.00	Sterling 1993	Sterling 1994	Donati and Borgognini-Tarli 2006
Daubentonia robustus		omnivore	14200.00	Jungers et al. 2008	Godfrey et al. 2004	Donati and Borgognini-Tarli 2006
Eulemur albifrons	cathemeral	frugivore	2310.00	Junge et al. 2009		Curtis 2006
Eulemur cinereiceps	cathemeral	frugivore	2250.00	Johnson et al. 2005; Mittermeier et al. 2010	Johnson et al. 2005; Mittermeier et al. 2010	Donati and Borgognini-Tarli 2006

Eulemur collaris	cathemeral	frugivore	2180.00	Donati et al., 2007		Donati and Borgognini-Tarli 2006
Eulemur coronatus	cathemeral	frugivore	1200.00	Terranova and Coffman, 1997		Donati and Borgognini-Tarli 2006
Eulemur flavifrons	cathemeral	frugivore	1900.00	Terranova and Coffman, 1997		Schwitzer et al. 2007
Eulemur fulvus	cathemeral	frugivore	1820.00	Rassmussen 1999		Donati and Borgognini-Tarli 2006
Eulemur macaco	cathemeral	frugivore	1820.00	Colquhoun 1997		Donati and Borgognini-Tarli 2006
Eulemur mongoz	cathemeral	frugivore	1043.00	Rassmussen 1999		Donati and Borgognini-Tarli 2006
Eulemur rubriventer	cathemeral	frugivore	2013.50	Glander et al. 1992		Donati and Borgognini-Tarli 2006
Eulemur rufifrons	cathemeral	frugivore	2188.84	Glander et al. 1992		Donati and Borgognini-Tarli 2006
Eulemur rufus	cathemeral	frugivore	1828.98	Junge et al. 2005		Donati and Borgognini-Tarli 2006
Eulemur sanfordi	cathemeral	frugivore	1850.00	Terranova and Coffman, 1997		Donati and Borgognini-Tarli 2006

Hadropithecus stenognathus	diurnal	omnivore	35400.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Hapalemur alaotrensis	diurnal	folivore	1530.41	Mittermeier et al., 2010		Mutschler et al. 1998
Hapalemur aureus	diurnal	folivore	1548.00	Glander et al. 1992		Tan 2000
Hapalemur griseus	diurnal	folivore	935.00	Glander et al. 1992		Tan 2000
Hapalemur meridionalis	diurnal	folivore	855.00	Mittermeier et al., 2010		Tan 2006
Hapalemur occidentalis	diurnal	folivore	900.00	Mittermeier et al., 2010		Tan 2006
Hapalemur simus	diurnal	folivore	2450.00	Tan 1999		Tan 2000
Indri indri	diurnal	folivore	6500.00	Glander and Powzyk 1998		Donati and Borgognini-Tarli 2006
Lemur catta	diurnal	frugivore	2245.00	Koyama 2008		Donati et al. 2013
Lepilemur aeeclis	nocturnal	folivore	988.64	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur ahmansonorum	nocturnal	folivore	610.00	Louis et al. 2006		
Lepilemur ankaranensis	nocturnal	folivore	608.01	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur betsileo	nocturnal	folivore	1150.00	Louis et al. 2006		
Lepilemur dorsalis	nocturnal	folivore	1087.50	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur edwardsi	nocturnal	folivore	978.75	Louis et al. 2006	Thalmann 2001	Donati and Borgognini-Tarli 2006

Lepilemur fleuretae	nocturnal	folivore	980.00	Louis et al. 2006		
Lepilemur grewcockorum	nocturnal	folivore	780.00	Louis et al. 2006		
Lepilemur hollandorum	nocturnal	folivore	1000.00	Louis et al. 2006		
Lepilemur hubbardorum	nocturnal	folivore	771.14	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur jamesorum	nocturnal	folivore	780.00	Louis et al. 2006		
Lepilemur leucopus	nocturnal	folivore	771.14	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur microdon	nocturnal	folivore	721.71	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur milanoii	nocturnal	folivore	720.00	Louis et al. 2006		
Lepilemur mittermeieri	nocturnal	folivore	988.64	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur mustelinus	nocturnal	folivore	852.70	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur otto	nocturnal	folivore	779.05	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur petteri	nocturnal	folivore	630.00	Louis et al. 2006		
Lepilemur randrianasoloi	nocturnal	folivore	920.00	Louis et al. 2006		
Lepilemur ruficaudatus	nocturnal	folivore	692.05	Louis et al. 2006	Ganzhorn 2002	Donati and Borgognini-Tarli 2006

Lepilemur sahamalazensis	nocturnal	folivore	741.48	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur scottorum	nocturnal	folivore	876.00	Louis et al. 2006		
Lepilemur seali	nocturnal	folivore	961.00	Lei et al. 2007		
Lepilemur septentrionalis	nocturnal	folivore	580.00	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Lepilemur tymerlachsoni	nocturnal	folivore	875.00	Louis et al. 2006		
Lepilemur wrightae	nocturnal	folivore	1150.00	Louis et al. 2006		
Megaladapis edwardsi	diurnal	folivore	85100.00	Jungers et al. 2008	Godfrey et al. 2012	Godfrey et al. 2006
Megaladapis grandidieri	diurnal	folivore	74300.00	Jungers et al. 2008	Godfrey et al. 2004	Godfrey et al. 2006
Megaladapis madagascariensis	diurnal	folivore	46500.00	Jungers et al. 2008	Godfrey et al. 2004	Godfrey et al. 2006
Mesopropithecus dolichobrachion	diurnal	folivore	13700.00	Jungers et al. 2009	Godfrey et al. 2012	Godfrey et al. 2006
Mesopropithecus pithecoides	diurnal	folivore	11300.00	Jungers et al. 2010	Godfrey et al. 2012	Godfrey et al. 2006
Microcebus arnholdi	nocturnal	omnivore	50.00	Louis et al. 2008		Donati and Borgognini-Tarli 2006
Microcebus berthae	nocturnal	omnivore	30.60	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus bongolavensis	nocturnal	omnivore	55.00	Mittermeier et al., 2010		Donati and Borgognini-Tarli 2006

Microcebus danfossi	nocturnal	omnivore	63.00	Olivieri et al. 2007		Donati and Borgognini-Tarli 2006
Microcebus gerpi	nocturnal	omnivore	70.00	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006
Microcebus griseorufus	nocturnal	omnivore	62.60	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus jollyae	nocturnal	omnivore	61.00	Louis et al. 2006		
Microcebus lehilahytsara	nocturnal	omnivore	39.00	Rasoloarison et al. 2013		Donati and Borgognini-Tarli 2006
Microcebus macarthurii	nocturnal	omnivore	53.70	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006
Microcebus mamiratra	nocturnal	omnivore	57.80	Radespiel et al. 2012		Donati and Borgognini-Tarli 2006
Microcebus margotmarshae	nocturnal	omnivore	41.00	Louis et al. 2008		
Microcebus marohita	nocturnal	omnivore	55.76	Rasoloarison et al. 2013		Donati and Borgognini-Tarli 2006
Microcebus mittermeieri	nocturnal	omnivore	59.32	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus murinus	nocturnal	omnivore	48.44	Schmid and Kappeler 1998		Donati and Borgognini-Tarli 2006

Microcebus myoxinus	nocturnal	omnivore	58.33	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus ravelobensis	nocturnal	omnivore	42.51	Randrianambinina et al. 2003		Donati and Borgognini-Tarli 2006
Microcebus rufus	nocturnal	omnivore	43.60	Louis et al. 2006	Atsalis 2007	Donati and Borgognini-Tarli 2006
Microcebus sambiranensis	nocturnal	omnivore	59.91	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Microcebus simmonsi	nocturnal	omnivore	50.91	Louis et al. 2006		Donati and Borgognini-Tarli 2006
Microcebus tavaratra	nocturnal	omnivore	1730.12	Yoder et al. 2000		Donati and Borgognini-Tarli 2006
Mirza coquereli	nocturnal	omnivore	289.67	Ganzhorn and Kappeler 1996	Ganzhorn and Kappeler 1996	Donati and Borgognini-Tarli 2006
Mirza zaza	nocturnal	omnivore	300.00	Kappeler et al. 2005		Donati and Borgognini-Tarli 2006
Pachylemur jullyi	diurnal	frugivore	11500.00	Godfrey et al. 2010	Godfrey et al. 2010	Godfrey et al. 2010
Palaeopropithecus ingens	diurnal	folivore	41500.00	Jungers et al. 2008	Godfrey et al. 2010	Godfrey et al. 2006
Palaeopropithecus maximus	diurnal	folivore	45800.00	Jungers et al. 2008	Godfrey et al. 2010	Godfrey et al. 2006
Phaner electromontis	nocturnal	omnivore	387.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010

Phaner furcifer	nocturnal	omnivore	450.00	Ganzhorn and Kappeler 1996	Ganzhorn and Kappeler 1996	Donati and Borgognini-Tarli 2006
Phaner pallescens	nocturnal	omnivore	327.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010
Phaner parienti	nocturnal	omnivore	360.00	Mittermeier et al., 2010	Mittermeier et al., 2010	Mittermeier et al., 2010
Propithecus candidus	diurnal	folivore	5500.00	Lehman et al. 2005	Lehman et al. 2005	Donati and Borgognini-Tarli 2006
Propithecus coquereli	diurnal	folivore	3700.00	Kappeler 1991		Donati and Borgognini-Tarli 2006
Propithecus coronatus	diurnal	folivore	3900.00	Mittermeier et al., 2010		Donati and Borgognini-Tarli 2006
Propithecus deckenii	diurnal	folivore	2810.00	Junge et al. 2005		Donati and Borgognini-Tarli 2006
Propithecus diadema	diurnal	folivore	5190.00	Irwin 2006	Irwin 2006	Donati and Borgognini-Tarli 2006
Propithecus edwardsi	diurnal	folivore	5742.50	Glander et al. 1992	Hemingway 1998	Donati and Borgognini-Tarli 2006
Propithecus perrieri	diurnal	folivore	4332.50	Lehman et al. 2005		Donati and Borgognini-Tarli 2006

Propithecus tattersalli	diurnal	folivore	3500.00	Meyers and Wright 1993	Irwin 2007	Donati and Borgognini-Tarli 2006
Propithecus verreauxi	diurnal	folivore	3190.00	Lewis and Kappeler 2005		Donati and Borgognini-Tarli 2006
Varecia rubra	diurnal	frugivore	3470.00	Vasey 2005		Donati and Borgognini-Tarli 2006
Varecia variegata	diurnal	frugivore	3665.00	Baden et al. 2008	Balko and Underwood 2005	Donati and Borgognini-Tarli 2006

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APPENDIX V

Supplemental materials to accompany Chapter Six

Survey methodology:

Survey personnel: I trained six Malagasy research assistants in the methods outlined below during the first three months of fieldwork and I conducted routine inter-observer reliability assessments with personnel throughout the study period to avoid observer drift. We conducted tests of distance and height estimates made by eye compared to measured values to ensure precision and accuracy in these data (all estimates +/-1m). I rotated all assistants to minimized systematic bias due to which observer recorded data.

Field data collection: *Lemur sampling*: I conducted lemur surveys during overlapping months among localities to reduce variation in abundance estimates due to the seasonality. Each locality was sampled during 2-3 months of each the wet and dry seasons. Three nocturnal species, *Microcebus rufus*, *Cheirogaleus crossleyi* and *C. sibreei* are less active or entirely dormant during the dry season, using daily torpor or hibernation to survive periods of food scarcity (Dausman et al. 2004, Blanco and Rahalinarivo 2010). Nocturnal sampling was decreased between May and July and the total survey efforts were adjusted for those species. For *Cheirogaleus*, survey effort included all surveys conducted between the first sighting of the year (between August and September) and the last sighting (May). For *Microcebus*, separate survey efforts were calculated for dry (May – September) and wet seasons. With my team of research assistants, I conducted diurnal and nocturnal surveys on transects using distance sampling techniques (Buckland et al. 2010), a standardized methodology for estimating primate abundance (e.g., Johnson and Overdorff 1999, Irwin et al. 2005, Lehman et al. 2007, Herrera et al. 2011). We made repeated surveys on each transect to increase the chances of detecting all species present in the area and gain accurate estimates of encounter rates (diurnal mean = 10 repetitions, range=5-30, nocturnal mean=5, range=2 - 30). We alternated the start position of transects with each repetition to avoid any systematic bias due to the time of the survey. Surveys were conducted during most weather conditions, except if conditions such as rain and fog decreased visibility to less than 25 meters. If weather conditions changed during the survey such that visibility decreased < 25m, the survey was terminated and the reduced survey effort was recorded. We walked slowly along transects in the morning (7:00-12:00hrs) and night (18:00-23:00) looking and listening for lemurs. During nocturnal surveys, we searched the forest with dim headlamps which reflect the 'eye-shine' of the lemurs due to the reflective *tapetum lucidum* in their eyes. Once a lemur was detected from eye-shine, we used powerful flashlights to accurately identify species. When lemurs were encountered, we collected the following standard survey data: time and location of sighting on the transect, species, distance to the first lemur sighted (estimated by eye), bearing from the transect (measured with a compass), demographics of encountered groups of lemurs, group spread (furthest distance among individuals in the encountered group), and geographic coordinates with a Garmin 62 hand-held GPS unit. The distance from the observer to the first animal sighted was converted to the perpendicular distance using the bearing from the transect. If multiple individuals were encountered, I added half the distance of the group spread to the perpendicular distance to account for under-estimating distances because the first individual sighted is most likely at the periphery of the group and thus the distance to the center of the group is half the spread (Buckland et al. 2010). These distances were small, and did not dramatically affect density estimates compared to those made from perpendicular sighting distances alone (results not shown).

Environmental gradients: I recorded elevation (meters above sea level) on transects every 100m using a GPS unit. I gathered data on habitat disturbance every 100m by recording any instances of the following disturbance types: evidence of cattle in the forest, cut trees and tree stumps from logging, evidence of local artisanal gold mining including dams and pools dug in rivers as well as mines on river banks, man-made traps set for animals, forest encampments, agricultural activity, and finally human use and occupation history as told by local residents native to the area, land owners, and forestry records at the Centre ValBio research station (CVB). The human habitat disturbance could be broadly classified into three levels: 0=near pristine: negligible signs of active human resource extraction, no record of past commercial use or human habitation; 1=light disturbance: few signs of active human resource extraction, past history of selective hardwood exploitation and/or agricultural use 30+ years ago or human habitation 70+ years ago; 2= heavy disturbance: active human disturbance including lumbar extraction, agriculture, gold-mining, temporary settlements, past human habitation 50+ years ago.

I measured the botanical composition and structure on transects using the point-centered-quarter method (Cottam and Curtis 1954, Ganzhorn 2003). At 100m intervals along the transects, a point sample was taken. The point was divided into quadrats and within each quadrat, the tree closest to the center of the point was sampled for one tree in each of four size classes based on diameter at breast height (DBH): 0-5cm, 5-10cm, 10-25cm, and 25+cm. If there was no tree in a size class within 10m radius from the point in any quadrat, that size class was recorded as lacking a tree. Trees were identified to the lowest taxonomic level possible by a team of four Malagasy research assistants trained in botany by CVB, the Missouri Botanical Garden, previous international research teams, and Malagasy forestry departments. Trees were identified based on leaf patterns, venation, and color, bark pattern, sap/latex production, and fruit and flower form when available. Trees in the field were recorded by Malagasy name and later translated to taxonomic Family, Genus and, where possible, species based on the extensive botanical database available at CVB. DBH was recorded with a measuring tape, while height, crown height and crown diameter were estimated by eye. Crown height was defined as the height from the first branches of the crown to the top of the tree. Crown diameter was defined as the maximum distance spanned by the branches of the tree. Observers were trained in height estimation by comparing estimates made by eye to those measured either with a measuring tape or a clinometer until observers were within a precision of +/-1m.

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SM Table 1. Functional traits of lemur species in the regional species pool. % leaves = percentage of leaves in the diet; AFR = age at first reproduction, in years; group size = mean number of individuals observed together in social units either from long-term studies or data collected during this study, ln mass = natural log of body mass. Data were taken from the literature.

Binomial name	**% leaves**	**AFR**	**group size***	**ln mass[1]**
Daubentonia madagascariensis	0[2]	4[3]	1.00	7.89
Varecia variegata	5[4]	1.6[3]	2.75	8.161
Hapalemur simus	90[5]	3	5.00	7.601
Hapalemur aureus	90[5]	3	2.00	7.313
Hapalemur griseus	85[5]	1.5	2.33	6.908
Eulemur rufifrons	25[6]	1.54	7.66	7.601
Eulemur rubriventer	10[6]	1.77	3.06	7.601
Lepilemur sp.	90[7]	1.63[8]	1.00	6.802
Microcebus rufus	0[9]	1[9]	1.00	3.807
Cheirogaleus sibreei	0[10]	2	1.14	5.493[11]
Cheirogaleus crossleyi	0[10]	2[12]	1.14	5.900[11]
Avahi peyrierasi	95[13]	2.58[8]	1.65	6.908
Propithecus edwardsi	50[14]	4[15]	3.62	8.412

*this study, estimated from survey data, except *H. simus* known from long-term study group (Centre ValBio unpublished data).

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Density analyses:

I used the program DISTANCE to estimate the detection probability from the perpendicular lemur sighting distances. I test the fit of the following functions to the data: uniform, half-normal, hazard-rate, each with cosine and simple polynomial terms. The best function was selected using the minimum Akaike information criterion corrected for small samples (AICc). Model adequacy was assessed using qqplots and goodness of fit tests as implemented in DISTANCE. The mean observed group size was used to estimate individual density from cluster density. I estimated a global detection probability and mean cluster sizes from all the data together, and estimated encounter rates and densities stratified by transect to obtain the densities per transect.

Supplementary results

Lemur species richness and density per transect.

The two bamboo lemur species not observed, *Hapalemur aureus* and *H. simus*, are known to occur at approximately three localities within RNP; their abundance in other areas of the park, however, is unknown. I did not observe the animals during our surveys or their characteristic feeding signs, and thus they were recorded as absent. *Daubentonia* was observed once on a single transect during the surveys, but characteristic feeding signs (bore marks in dead wood) were found on every transect and thus we inferred them to be present but with low abundance. I use a value of 0.001 individuals / km^2 for *Daubetonia* at all transects to reflect their presence but low relative abundance. Further, *Cheirogaleus* species are difficult to distinguish from survey data alone. A concomitant study on *Cheirogaleus* using trapping data suggested that at the two localities where *C. sibreei* was present, it was sympatric with *C. crossleyi* and the capture frequency of each species was roughly equal, suggesting the two species were approximately equal in abundance (unpub. personal data). Thus, I inferred the individual density of *Cheirogaleus* from the transect survey data and, at the two localities where the species are sympatric, assigned half the total *Cheirogaleus* density to each species. Finally, on three transects (VOF, VOG, and VOH) nocturnal survey effort was too low (two repetitions) to reliably estimate abundance. I imputed the mean density for the locality at which the transect was located to fill missing values of each nocturnal species observed during the two surveys. Thus, the presence of the species was confirmed during surveys, but the abundance was imputed.

Supplementary results table. Mean estimated individual density (ind/km^2) of each lemur species on each transect. *D. mada.ensis* = *Daubentonia madagascariensis*.

Transect	*D. mada.ensis*	*V. variegata*	*H. simus*	*H. aureus*	*H. griseus*	*E. rufifrons*	*E. rubriventer*	*Lepilemur* sp.	*M. rufus*	*C. sibreei*	*C. crossleyi*	*A. peyrierasi*	*P.edwardsi*
AA	0.01	0.00	0.00	0.00	1.70	0.00	8.04	6.25	42.64	2.07	2.07	34.26	11.81
AB	0.01	0.00	0.00	0.00	0.00	0.00	1.91	7.37	73.53	9.77	9.77	44.47	9.51
AC	0.01	0.00	0.00	0.00	1.12	0.00	3.99	12.53	78.91	12.45	12.45	20.61	6.01
AD	0.01	0.00	0.00	0.00	0.00	0.00	0.00	4.17	13.12	0.00	20.71	34.26	4.72
AE	0.01	0.00	0.00	0.00	2.21	0.00	0.00	10.53	56.58	0.00	16.01	35.67	7.08
AF	0.01	0.00	0.00	0.00	3.68	7.08	10.88	10.53	56.58	0.00	16.01	35.67	7.87
AG	0.01	0.00	0.00	0.00	0.00	0.00	4.48	35.71	74.97	8.87	8.87	48.95	16.19
MA	0.01	0.00	0.00	0.00	1.53	0.00	8.83	3.56	84.10	7.08	7.08	23.43	0.00
MB	0.01	0.00	0.00	0.00	2.61	0.00	5.03	25.00	59.04	2.07	2.07	6.85	0.00
MC	0.01	0.00	0.00	0.00	5.35	0.00	0.00	10.42	32.80	0.00	0.00	51.40	0.00
MIA	0.01	0.00	0.00	0.00	1.95	37.76	2.51	0.00	30.07	0.00	39.69	5.71	5.86
MIB	0.01	0.00	0.00	0.00	0.00	76.10	5.30	0.00	18.22	0.00	57.52	3.81	8.84
MIC	0.01	0.00	0.00	0.00	4.84	14.18	10.37	0.00	20.87	0.00	33.88	6.23	3.46
MID	0.01	0.00	0.00	0.00	0.00	9.32	6.82	4.63	10.93	0.00	25.31	3.81	1.89
MIE	0.01	0.00	0.00	0.00	2.18	15.35	25.26	0.00	49.20	0.00	46.59	14.28	10.92
MIF	0.01	0.00	0.00	0.00	5.07	0.00	16.31	0.00	13.46	0.00	14.87	21.09	14.51
VA	0.01	0.00	0.00	0.00	0.00	15.03	5.41	0.00	132.02	0.00	30.67	22.17	0.00
VB	0.01	1.60	0.00	0.00	0.00	16.97	0.00	0.00	34.99	0.00	18.41	35.53	13.64
VC	0.01	3.15	0.00	0.00	1.42	19.50	4.51	1.75	98.53	0.00	13.65	49.05	10.07
VD	0.01	3.33	0.00	0.00	2.39	21.17	6.35	0.00	59.56	0.00	30.96	25.66	5.67
VE	0.01	0.81	0.00	0.00	2.89	14.24	12.31	0.00	51.70	0.00	21.76	5.90	6.86
VF	0.01	1.28	0.00	0.00	0.00	9.02	9.74	1.96	72.27	0.00	12.55	16.09	10.87
VG	0.01	2.78	0.00	0.00	2.50	9.84	5.31	3.58	21.87	0.00	21.46	29.41	14.82
VOA	0.01	0.00	0.00	0.00	4.94	0.00	7.96	4.17	90.20	0.00	5.18	6.85	1.60
VOB	0.01	0.00	0.00	0.00	0.00	2.29	11.28	5.21	104.96	0.00	4.14	0.00	5.45
VOC	0.01	0.00	0.00	0.00	0.00	0.00	4.51	1.49	98.40	0.00	3.45	0.00	5.45
VOD	0.01	0.00	0.00	0.00	7.41	0.00	7.96	0.00	103.08	0.00	0.00	6.85	6.41
VOE	0.01	0.00	0.00	0.00	4.94	0.10	11.94	0.00	87.46	0.00	5.18	4.89	3.21

VOF	0.01	0.00	0.00	0.00	10.50	0.00	0.00	2.51	75.21	0.00	3.45	3.54	0.00
3.G	VOG	0.01	0.00	0.00	0.00	0.00	4.90	0.00	2.51	75.21	0.00	3.45	3.54
3.H	VOH	0.01	0.00	0.00	0.00	0.00	9.81	4.83	2.51	75.21	0.00	3.45	3.54

Supplementary results table. Loadings of original dendrometrics on the first principle component, which summarizes 70% of the variation in the forest structure variables.

Variable	**PC1**
Diameter at breast height	0.37
Tree height	0.53
Crown height	0.51
Crown diameter	0.57

Supplementary results table. Results of phylogenetic community structure analysis comparing the observed mean nearest taxon distance (MNTD) to that expected under a null model that maintains species prevalence and randomizes abundances. P values < 0.05 indicate phylogenetic clustering, > 0.95 is overdispersed.

Transect	Species richness	MNTD observed	MNTD null mean	MNTD null SE	MNTD observed rank	MNTD effect size	p
1.A	9.00	0.66	0.72	0.12	297.00	-0.51	0.30
1.B	8.00	0.66	0.71	0.11	304.00	-0.46	0.30
1.C	9.00	0.69	0.72	0.12	361.00	-0.31	0.36
1.D	6.00	0.67	0.71	0.12	334.00	-0.38	0.33
1.E	7.00	0.74	0.72	0.11	580.00	0.15	0.58
1.F	9.00	0.66	0.72	0.12	314.00	-0.47	0.31
1.G	8.00	0.72	0.72	0.12	500.00	-0.04	0.50
2.A	8.00	0.58	0.73	0.12	95.00	-1.26	0.10
2.B	7.00	0.50	0.72	0.11	30.00	-1.93	0.03
2.C	8.00	0.61	0.73	0.11	128.00	-1.02	0.13
2.D	8.00	0.64	0.72	0.12	217.00	-0.67	0.22
2.E	8.00	0.61	0.72	0.11	140.00	-1.02	0.14
2.F	7.00	0.64	0.71	0.11	229.00	-0.63	0.23
3.A	8.00	0.78	0.73	0.11	683.00	0.41	0.68
3.B	7.00	0.77	0.73	0.12	652.00	0.32	0.65
3.C	6.00	0.84	0.73	0.12	856.00	0.97	0.86
3.D	6.00	1.04	0.73	0.13	989.00	2.47	0.99
3.E	8.00	0.72	0.73	0.12	445.00	-0.09	0.45
3.F	6.00	0.87	0.73	0.12	890.00	1.15	0.89
3.G	6.00	0.85	0.73	0.11	874.00	1.08	0.87
3.H	7.00	0.74	0.73	0.12	569.00	0.10	0.57
4.A	6.00	0.79	0.72	0.11	743.00	0.61	0.74
4.B	7.00	0.68	0.72	0.11	328.00	-0.39	0.33
4.C	10.00	0.65	0.72	0.12	255.00	-0.63	0.26
4.D	9.00	0.64	0.73	0.11	206.00	-0.82	0.21

4.E	9.00	0.63	0.72	0.11	203.00	-0.80	0.20
4.F	9.00	0.67	0.73	0.11	275.00	-0.57	0.28
4.G	10.00	0.61	0.73	0.11	141.00	-1.01	0.14
5.A	8.00	0.81	0.73	0.12	790.00	0.72	0.79
5.B	8.00	0.86	0.71	0.11	917.00	1.29	0.92
5.C	5.00	1.12	0.71	0.11	1000.00	3.51	1.00

Results of simulations. The power of the mean nearest taxon distance to detect significant deviations from the null expectation expressed as the percentage of communities that were inferred to be significantly different from the null expectation. Weighted: MNTD weighted by simulated abundances. False positive is the percentage of simulated communities with no phylogenetic signal that were inferred to deviate from the null distribution.

n tips	**clustered power weighted**	**clustered power non-weighted**	**overdispersed power weighted**	**overdispersed power unweighted**	**false positive rate weighted clustered**	**false positive rate weighted overdispersed**	**false positive rate nonweighted clustered**	**false positive rate nonweighted overdispersed**
5	20%	0%	2%	0%	4%	2%	0%	2%
10	22%	13%	4%	6%	6%	5%	3%	6%
15	38%	30%	7%	3%	7%	4%	3%	4%
25	35%	33%	5%	7%	5%	5%	4%	5%
50	43%	41%	7%	16%	5%	4%	6%	4%
75	79%	71%	1%	2%	4%	5%	3%	5%
100	74%	63%	3%	10%	3%	4%	5%	4%