



The Effects of Biogeography and Biotic Interactions on Lemur Community Assembly

James P. Herrera^{1,2,3} 

Received: 28 March 2017 / Accepted: 23 May 2017 / Published online: 21 July 2017
© Springer Science+Business Media, LLC 2017

Abstract Geographic patterns of biodiversity result from broad-scale biogeographic and present-day ecological processes. The aim of this study was to investigate the relative importance of biogeographic history and ecology driving patterns of diversity in modern primate communities in Madagascar. I collected data on endemic lemur species co-occurrence from range maps and survey literature for 100 communities in protected areas. I quantified and compared taxonomic, phylogenetic, and functional dimensions of intra- and intersite diversity. I tested environmental and geographic predictors of diversity and endemism. I calculated deforestation rates within protected areas between the years 2000 and 2014, and tested if diversity is related to forest cover and loss. I found the phylogenetic structure of lemur communities could be explained primarily by remotely sensed plant productivity, supporting the hypothesis that there was ecological differentiation among ecoregions, while functional-trait disparity was not strongly related to environment. Taxonomic and phylogenetic diversity also increased with increasing topographic heterogeneity. Beta diversity was explained by both differences in ecology among localities and potential river barriers. Approximately 3000 km² were deforested in protected areas since the year 2000, threatening the most diverse communities (up to 31%/park). The strong positive association of plant productivity and topographic heterogeneity with lemur diversity indicates that high

Handling Editor: Joanna M. Setchell

Electronic supplementary material The online version of this article (doi:[10.1007/s10764-017-9974-9](https://doi.org/10.1007/s10764-017-9974-9)) contains supplementary material, which is available to authorized users.

✉ James P. Herrera
jherrera@amnh.org

¹ Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA

² Division of Vertebrate Paleontology, American Museum of Natural History, New York, NY 10024, USA

³ Richard Gilder Graduate School, American Museum of Natural History, New York, NY 10024, USA

productivity, rugged landscapes support greater diversity. Both ecology and river barriers influenced lemur community ecology and biogeography. These results underscore the need for focused conservation efforts to slow the loss of irreplaceable evolutionary and ecological diversity.

Keywords Beta diversity · Deforestation · Geographic barriers · Macroecology · Phylogenetic community ecology · Species richness

Introduction

Geographic patterns of species distributions reflect ecological and evolutionary processes driving the distribution and diversity of life (Smith *et al.* 2014). Biogeographic events shape the regional species pools from which local communities are assembled (Mittelbach and Schemske 2015; Electronic Supplementary Material [ESM] Fig. S1). Local communities are further modified by environmental filtering, including resource limitation, and biotic interactions with sympatric species (Cavender-Bares *et al.* 2009). Alternative hypotheses about macroevolutionary processes driving community diversity can be tested based on the phylogenetic and functional similarities among co-occurring species (alpha diversity) and among localities (beta diversity) (Graham and Fine 2008; Price *et al.* 2014). Taxonomic diversity reflects the number of co-occurring species, which is taken as a correlate of productivity and is indicative of diversity hotspots (Hurlbert and Jetz 2007), but is silent on the evolutionary history of functional similarity of those species (Graham and Fine 2008). Phylogenetic diversity and community structure summarize the total evolutionary history represented by the species in a community, and whether those species are more or less closely related to each other than expected by random community assembly (Faith 1992; Webb 2000). Functional diversity quantifies how disparate the traits of species in a community are, reflecting the range of niches occupied (Devictor *et al.* 2010). Functional diversity is often assumed to be positively related to phylogenetic diversity but this assumption is not always met (Fergnani and Ruggiero 2015; Mayfield and Levine 2010), making it essential to quantify functional traits. By quantifying the taxonomic, phylogenetic, and functional diversity of communities, it is possible to tease apart the relative roles of environmental effects and interspecies competition on community assembly (Helmus *et al.* 2007).

Madagascar is renowned for its high diversity of endemic biota, which has been shaped by landscape changes in the deep and recent past (Ohba *et al.* 2016; Samonds *et al.* 2013). Paleoclimatic reconstructions suggest that Madagascar's climate was cooler, drier, less geographically variable, and less seasonal at the Cretaceous/Paleocene boundary than today but that the overall distribution of ecoregions was not significantly different from today (Ohba *et al.* 2016). More recent climate oscillations, documented by Pleistocene/Holocene pollen records, included periodic fluctuations between woodland and grassland species (Burney *et al.* 2004), and evidence of climate variability associated with the El Niño Southern Oscillation in the last ca. 3000 years (Brook *et al.* 1999). The recent spread of grasslands has been linked to drought conditions in the last 1000 years (Virah-Sawmy *et al.* 2010). In contrast to natural habitat change, isotopic evidence preserved in stalagmites and vertebrate subfossils indicates that there was no change in precipitation that could explain the shift from C₃

woodland-associated plants to C₄ grasses at around that time (Burns *et al.* 2016; Crowley *et al.* 2016). More recent analyses of stalagmites suggest the shift to grasslands postdated dry periods and was actually preceded most recently by warm, wet conditions and an archaeological record of human settlements (Voarintsoa *et al.* 2017). Thus, natural climate change has shaped the evolution of Madagascar's endemic biota in deep and recent times, while human activities have modified the natural landscape in the last ca. 1000 years.

Debate surrounds the evolutionary processes driving speciation in Madagascar. Competing hypotheses center on the roles of adaptive evolution, such as ecological diversification related to habitat suitability and niche partitioning, and vicariance events, especially due to physical dispersal barriers (Brown *et al.* 2014; Ganzhorn *et al.* 2006; Vences *et al.* 2009). Three major hypotheses related to deep-time biogeographic processes and ecological interactions are proposed to explain evolution on Madagascar. Predictions derived from these biogeographic hypotheses for the expected patterns of taxonomic, phylogenetic, and functional alpha and beta diversity (Fig. 1) provide a framework for testing the competing hypotheses in Madagascar (see ESM for details). These hypotheses are not exhaustive or mutually exclusive, but they are among the main mechanisms proposed for evolution in Madagascar (Brown *et al.* 2014).

The first hypothesis, the ecoregions hypothesis, posits species diverged as a result of adaptation to wet vs. dry environments related to rainfall gradients across the island (Koechlin 1972). Under the ecoregions hypothesis, taxonomic, phylogenetic, and

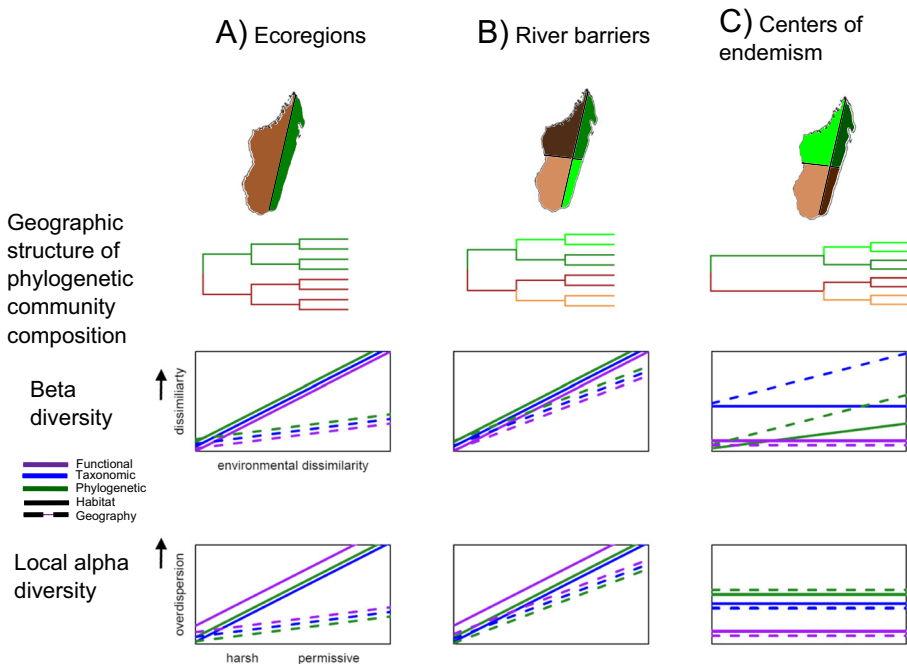


Fig. 1 Illustration of predictions for patterns of beta diversity and local alpha diversity in lemurs at two geographic scales under three hypotheses of biogeographic evolution. The slope lines of the relationships among beta diversity measures refer to habitat variables (*solid lines*) and geographic distance (*dashed lines*). **a** Ecoregions hypothesis. **b** River barriers hypothesis. **c** Pleistocene centers of endemism hypothesis.

functional beta diversities are predicted to be positively related to rainfall gradients; i.e., increasing dissimilarity in habitat types due to rainfall gradients is predicted to be related to increasing dissimilarity in lemur communities. Under this hypotheses, several predictions can be made concerning alpha diversity based on principles of community ecology. Within communities (alpha diversity), competition and resource limitation are hypothesized to be the primary drivers of community assembly (Cavender-Bares *et al.* 2009; Ganzhorn 1997). Taxonomic, phylogenetic, and functional alpha diversities are predicted to be positively related if competition is the driving factor (Cavender-Bares *et al.* 2009) and if traits are phylogenetically conserved (Mayfield and Levine 2010). Alpha diversities and endemism are predicted to increase with increasing resource abundance, area, and topographic heterogeneity because these factors increase ecological opportunity for niche partitioning while small, resource-limited, homogeneous environments are predicted to limit diversity (Kerr and Packer 1997). Geographic dispersal limitation is predicted to be minimal, because the main cause of diversity gradients is the environment.

The second hypothesis, the riverine dispersal barrier hypothesis suggests that, in addition to the ecological differentiation evident between wet, dry, and arid ecoregions, several key rivers were dispersal barriers within each ecoregion (Martin 1972; Pastorini *et al.* 2003). In this hypothesis, the presence of physical barriers is predicted to be positively related to lemur beta diversity and endemism in addition to environment, because of the dispersal limitation effects of the barrier.

The third hypothesis, the Pleistocene centers of endemism hypothesis, views rivers with high elevation headwaters as refuges of wet habitat and corridors for dispersal, while rivers with low elevation headwaters would have been isolated watersheds facilitating allopatric speciation during the Quaternary (Mercier and Wilmé 2013; Wilmé *et al.* 2006). Because of the purportedly recent time scale, i.e., Pleistocene, this hypothesis predicts that taxonomic beta diversity is higher than phylogenetic beta diversity because of high turnover among localities of sister species that were only recently separated. Phylogenetic alpha diversity is predicted to be high because sister species have allopatric distributions, making the co-occurrence of close relatives infrequent. Key to discriminating between the river dispersal barrier hypothesis and the Pleistocene centers of endemism hypothesis is that under the centers of endemism hypothesis, alpha diversity and endemism are not predicted to be related to environmental factors because community assembly was due to allopatric separation by physical barriers, rather than ecological adaptation.

Previous research has shown that lemur species richness is higher in wet than in dry forests, related to concordant patterns in tree species diversity, supporting an effect of ecological factors on community assembly (Ganzhorn *et al.* 1997). Further, studies have provided evidence that competition structures communities because species in communities occupy unique functional guilds (Fox's assembly rules, Ganzhorn 1997), and there is fine-scale niche partitioning within communities and within guilds (Ganzhorn 1988). Studies have shown that taxonomic beta diversity consistently indicates an east vs. west dichotomy (Ganzhorn *et al.* 1999; Kamilar 2009; Kamilar and Muldoon 2010). Further, geographic distance as well as environmental dissimilarity were positively related to lemur beta diversity (Bannar-Martin 2014; Beaudrot and Marshall 2011). Research on the phylogenetic alpha diversity of lemur communities suggested phylogenetic diversity was mostly no different from null expectations, with

some communities consisting of distantly related species (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). These studies reveal that both geography and ecology influence lemur communities, but the relative effects of each are unclear.

In addition to the three biogeographic and ecological hypotheses, recent anthropogenic habitat changes have affected lemur communities. A fourth hypothesis concerning the potentially confounding effects of habitat loss is that habitat loss will be negatively related to species richness, such that habitats with higher deforestation will have lower species richness than habitats with lower deforestation (Newbold *et al.* 2015). Larger protected areas are predicted to have higher diversity than smaller protected areas because of the positive relationship between species richness and area found for many taxa (Matthews *et al.* 2014). While there is a striking diversity of ca. 100 lemur species today, at least 17 more species existed before the arrival of people between 2000 and 4000 years ago (Godfrey *et al.* 2010; Goodman and Jungers 2014). Although the change from C₃ woodland plants to C₄ grass communities in the southeast was related to natural drought and was coincident with lemur declines (Virah-Sawmy *et al.* 2010), an abundance of evidence points to the effect of human-induced changes to the landscape and associated extinctions of large-bodied lemurs (Burns *et al.* 2016; Crowley *et al.* 2016). Further, lemur hunting is inferred from clear evidence of human butchery on lemur bones (Perez *et al.* 2005). The deleterious effects of human activities on lemur diversity continue today; 95% of lemurs are threatened with extinction as a result of habitat loss and hunting (Schwitzer *et al.* 2014). The historical extent of anthropogenic deforestation is debated, but it is clear that since 1950, forest area has declined by 40–50%, and 10% of the island is forested (Harper *et al.* 2007; Scales 2014). Given that most lemurs are forest dependent, this decrease in suitable habitat is a leading threat (Schwitzer *et al.* 2014) and may have cascading effects in ecosystems because lemurs are important pollinators (Wright and Martin 1995), seed dispersers (Razafindratsima *et al.* 2014), and prey for apex predators (Karpanty and Wright 2007). To preserve ecosystem resilience, it is important to understand how lemur community structure is affected by habitat loss.

In this study, I tested biogeographic hypotheses to explain the diversity and distribution of lemurs, with explicit predictions that disentangle covarying factors (Fig. 1). I generated a community composition matrix for 98 species in 100 protected areas (Fig. 2) and quantified the topography, climate, plant productivity, geography, and forest loss of protected areas from available databases (Hansen *et al.* 2013; Heinsch *et al.* 2003; Hijmans *et al.* 2005). Based on a recently inferred near-complete phylogeny (Herrera and Dávalos 2016) and functional traits characterizing niche partitioning, I quantified phylogenetic and functional dimensions of lemur diversity. By integrating multiple dimensions of community diversity across scales, it is possible to tease apart the associations between lemur diversity, dispersal barriers, and environmental gradients. I tested if variation in taxonomic, phylogenetic, and functional diversity and phylogenetic endemism among and within communities could be explained by geographic barriers, local environments, plant productivity, and/or interspecies competition. I then measured deforestation rates for each of the communities to quantify the threat level to those communities due to habitat loss.

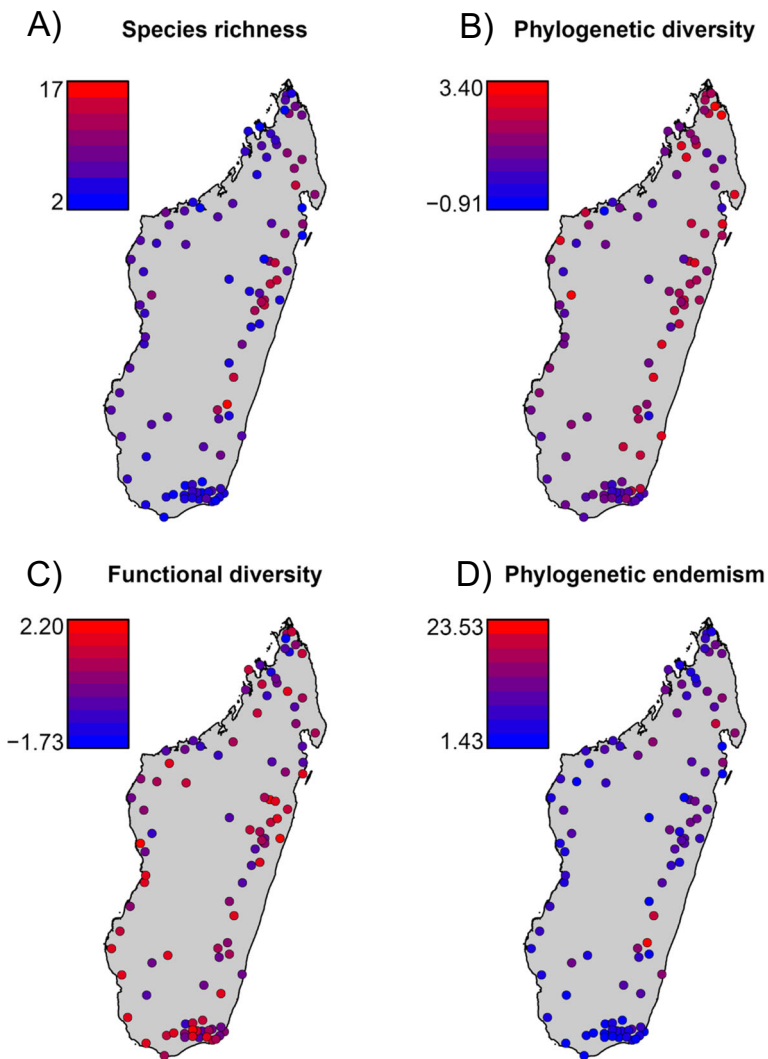


Fig. 2 Geographic distribution of four dimensions of lemur biodiversity. The centroids of protected areas are color-coded to indicate the (a) taxonomic (species richness), (b) phylogenetic and (c) functional alpha diversity, and (d) phylogenetic endemism. Phylogenetic/functional diversity was measured using mean nearest taxon distance (MNTD). Positive values: co-occurring species are less similar than chance; negative values: more similar than chance; zero: random assembly.

Methods

The workflow of this study involved first creating a database of Madagascar bioregions and protected areas, lemur geographic distributions, and environmental layers. I then calculated taxonomic, phylogenetic, and functional beta diversity among pairs of protected areas and alpha diversity within protected areas. To test the effects of climate, resource abundance, and abiotic dispersal barriers on community ecology and biogeography, I correlated climate, geographic, and plant productivity variables with

community diversity. I calculated the area and percent forest cover in the year 2000 and the loss of forest until 2014 (Hansen *et al.* 2013) to estimate the total area and percent forest loss in Madagascar and within protected areas.

Taxa and Phylogeny

Lemur taxonomy is in flux, and the number of species recognized has risen from ca. 50 recognized by some scholars in 2006 (Ganzhorn *et al.* 2006) to >100 recognized in the most recent compilation (Mittermeier *et al.* 2010). Several new species have been described since then. Some of the newly erected taxa were previously subspecies, while others are “cryptic” species that had not been studied intensively until recently. These revisions have been met with skepticism (Markolf *et al.* 2011; Tattersall 2007), but studies that have rigorously tested species hypotheses based on genetic, phenotypic, and geographic data have typically found support for the newly described species (Markolf *et al.* 2013; Radespiel *et al.* 2011; Yoder *et al.* 2005, 2016). Among the newly erected species, some were later subsumed based on multidimensional data, e.g., *Cheirogaleus* (Groeneveld *et al.* 2009). In this article, I followed the taxonomy of Mittermeier *et al.* (2010), with the addition of *Microcebus gerpi* (Radespiel *et al.* 2011), *M. tanosi*, and *M. marohita* (Rasoloarison *et al.* 2013). I used a near-complete phylogeny with ca. 90% of living lemurs (Herrera and Dávalos 2016). Species missing from the original phylogeny (16 species) did not have genetic loci comparable to those used in the phylogenetic inference, but were proposed based on mitochondrial genetic divergence (Lei *et al.* 2008; Louis 2006). 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 using functions in the R package ape (Paradis *et al.* 2004). These species were from the genera *Lepilemur*, *Phaner*, and *Avahi*. For *Lepilemur* and *Avahi*, 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*, *P. furcifer* was the only species in the original phylogeny, and three congeners were added to it between 0.5 and 2.5 million years ago (Ma) based on the upper credible interval of divergence time estimates from mitochondrial genomes (Louis and Lei 2016). 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 (see ESM).

Functional Traits

Sympatric species diverge in traits related to diet and activity pattern, suggesting they are important in niche partitioning that may affect community composition (Ganzhorn 1988; Ossi and Kamilar 2006). For example, while multiple folivorous species are locally sympatric, the species have different diel patterns and some feed on leaves with high tannin content, while others feed on leaves high in alkaloids (Ganzhorn 1988). Body size is related to many other traits of species, e.g., life history (Smith and Jungers 1997), and thus I include body size in the trait data to capture variation in these other

traits. Data were compiled from the literature on the following variables: 1) body size (natural log, grams) 2) diet category (folivore, frugivores, omnivore), and 3) activity pattern (diurnal, nocturnal, cathemeral; ESM Table SI). Detailed natural history data were not available for many newly described species, especially in the genera *Avahi*, *Lepilemur*, and *Microcebus*. I took data for those taxa from Mittermeier *et al.* (2010) and by generalizing from well-studied congeners assumed to have similar niches. Diet information was available for these genera as follows: folivory has been documented in 3 out of 26 *Lepilemur* and 5 of 9 species of *Avahi*, and omnivory was documented for 1 out of 4 species of *Phaner* and 6 out of 20 *Microcebus* species.

I defined five biogeographic regions based on a simplified delineation of ecoregions subdivided by river barriers (Martin 1972; Pastorini *et al.* 2003). I georeferenced the maps from Pastorini *et al.* (2003) in a geographic information systems (GIS) database using QGIS (Quantum GIS Development Team 2015), with eight georeference points used to maximize the fit of the map to the GIS (ESM Fig. S2). All layers used the WGS 84 decimal latitude/longitude geographic coordinate reference system unless otherwise noted. The bioregions were central highlands (CH, based on georeferenced limits from Pastorini *et al.* 2003, elevational limit ca. 1100 m in the east and 500 m in the west/south), north east (NE) and southeast (SE) separated by the Onive–Mangoro river system, southwest (SW, labeled W2 in Pastorini *et al.* 2003) and northwest (NW, combining W1, NW, X, and N from Pastorini *et al.* 2003) separated by the Tsiribihina River. The NE and NW regions were delineated based on the georeferenced map of Pastorini *et al.* (2003) for the divide that they suggest for their northern region, between the Manambato and Mahavavy Rivers. The divide between the SE and SW regions was the Anosy mountain chain. Five simplified bioregions were used, rather than seven as originally proposed (Martin 1972), or more as suggested by some authors (Wilmé *et al.* 2006), because the sample size of protected areas within each region becomes too small with increasing partitioning of regions. These ecoregion designations were used to derive the “species pool” or the assemblage of species that could potentially colonize a protected area within the region (Swenson *et al.* 2006). The ecoregions were also used as a random-effect treatment in linear mixed effects models predicting lemur alpha diversity from environmental variables, to account for any nonindependence among protected areas owing to being in the same region.

Local Communities

I chose protected areas to quantify species richness in local communities, the scale at which individuals of multiple species interact and potentially compete for resources. Protected areas are delineated tracts of forest that had been inventoried for lemurs and thus could be verified, and previous studies in Madagascar have used protected areas as their local communities, making results of this study directly comparable. I obtained polygon shapefiles of 138 protected areas around Madagascar from the organization CIRAD (<http://madagascar.cirad.fr/recherche-en-partenariat/dispositifs-de-recherche-et-de-formation-en-partenariat/forets-et-biodiversite-a-madagascar>), which largely built on the areas proposed by Kremen *et al.* (2008). I modified the number of features in the protected area polygons from the original files to include only those protected areas with lemur species richness >2, to omit protected areas that were predominantly marine, and to include one reserve not in the original shapefile (Berenty Private

Reserve; *Eulemur* was not included in the Berenty presence/absence data because it was introduced). In this process, I retained 100 protected areas from the original file (ESM File 1, Fig. S2). I estimated the area of each protected area using the *poly.areas* function in the R package GISTools (Brunsdon and Chen 2014; R Core Team 2014) and a UTM transformed shapefile of protected areas. The results presented here should be interpreted with the caveat that protected area boundaries may change in the future, and though the shapefiles used in this study are reliable, the official boundaries of protected areas change as the protected area system evolves over time, and the delineation based on a GIS may depart from the protected area limits on the ground. However, analyses with a reduced set of 50 protected areas from Kremen *et al.* (2008) produced qualitatively similar results (see ESM).

Lemur Distributions

To create species co-occurrence matrices at regional and protected area scales, I obtained polygon shapefiles of extant lemur distribution maps from the IUCN terrestrial mammal database (<http://www.iucnredlist.org/technical-documents/spatial-data>). I verified each lemur range against original and secondary sources to confirm the limits of species distributions (Kamilar and Muldoon 2010; Mittermeier *et al.* 2010; Muldoon and Goodman 2015), editing polygons where necessary based on primary literature. I tabulated species presence/absence matrices for each protected area and region using the *intersect* function in the R package raster (Hijmans 2015). Co-occurrence matrices and estimates of species richness based solely on range maps vary depending on methods, scale, and the quality of maps (Graham and Hijmans 2006; Hurlbert and Jetz 2007). Expert-drawn range maps tend to overestimate diversity because they represent extent of occurrence, rather than area of occupancy (Hurlbert and Jetz 2007). Because of these limitations, I cross-validated co-occurrence matrices based on maps with literature sources of ground-truthed surveys at the protected areas (literature review conducted between January 16, 2016 and 1/26/2016, ESM Table SII). I obtained 44 papers and reports published between 1997 and 2016, with the earliest lemur surveys conducted in 1975 and most recent in 2015, and 66% of surveys were performed between 2000 and 2015. This review was a thorough evaluation of the available information on lemur occurrences in protected areas, representing our current published knowledge. Discrepancies between presence/absence records based on the range maps and surveys were handled case-by-case, with the information from surveys favored over range maps, as indicated in the SM (Hurlbert and Jetz 2007).

Environmental Variables

To quantify the environmental factors predicted to affect lemur community composition, I obtained environmental data from the WorldClim raster data layers (30 arc-second resolution, Hijmans *et al.* 2005). I also included layers of primary plant productivity. The Normalized Difference Vegetation Index (NDVI) was generated from the MODIS imagery of the NASA Terra satellite (<http://neo.sci.gsfc.nasa.gov>). 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 interannual variation. In addition to the wet and dry season

NDVI variables, I included a measure of annual net primary productivity generated by the MODIS project (<http://www.ntsug.umd.edu/project/mod17>). I extracted productivity, climate, and topography variables for each protected area from the MODIS and WorldClim rasters using the *extract* function in raster to calculate unweighted means of environmental variables for each protected area. For elevation, I calculated the mean as well as the standard deviation of elevation within the protected area to quantify topographic variability as a predictor. After eliminating variables that were correlated with $r \geq |0.90|$ (ESM Table SVIII), I retained the following environmental variables because they characterize habitats well and minimize correlation among independent variables: BIO3, isothermality; BIO4, temperature seasonality; BIO5, maximum temperature of warmest month; BIO6, minimum temperature of the coldest month; BIO7, temperature annual range; BIO11, mean temperature of the coldest quarter; BIO12, annual precipitation; BIO15, precipitation seasonality; BIO16, precipitation of wettest quarter; BIO18, precipitation of warmest quarter, mean altitude, standard deviation of altitude, wet and dry season NDVI, net primary productivity, area, percent forest cover, and percent forest loss. I also used the latitude and longitude of the protected area centroids as variables because geographic location may capture geographic structuring not included in the other variables, e.g., underlying geology. Latitude and longitude were also used to create a geographic distance matrix and to test for spatial autocorrelation by including a distance decay matrix in linear regressions. All the data for each protected area are available in the ESM (ESM Table SIII).

River Barriers

To quantify the effect of river barriers, I created raster layers that represented landscape resistance due to river barriers. I converted the major rivers shapefile from Brown *et al.* (2014) to a raster layer using the function *rasterize* from raster, and derived a transition matrix among cells where transition among nonriver cells was 1 and transition between nonriver and river cells was 0 to represent impassable barriers, as suggested by the riverine barrier and centers of endemism hypotheses (using the function *transition* from raster with the directions argument set to 8). I then calculated the least-cost distance among protected area centroids, specifying that the minimum value from each of the 8 surrounding cells be taken for the transition matrix (functions *geoCorrection* and *costDistance* from the package gdistance, van Etten 2012).

Forest Loss

To calculate forest loss in each protected area, I obtained the data products from (Hansen *et al.* 2013) for the granules covering Madagascar. The layers included the forest cover in the year 2000, as well as the forest loss between 2000 and 2014. For each dataset, I merged the three granules (*merge* function in the raster package) and converted them to UTM projection for area calculation (*projectRaster* function in raster, with the coordinate reference system +proj = utm + zone = 38S + ellps = WGS84, method = bilinear for the

continuous data raster of forest cover, and method = ngb for the categorical data layer of loss [0 or 1]). I used the *extract* function in raster to extract the values of pixels (% tree cover for forest cover, 0 or 1 for loss) for each protected area. I then calculated the total forest cover in the year 2000 for each protected area as the number of pixels with $\geq 50\%$ canopy cover within the boundaries of the protected area, and calculated the percentage of pixels within each protected area with loss. Area was calculated based on the size of the pixels ($26.4 \text{ m} \times 27.7 \text{ m}$). The 50% canopy cover threshold was chosen based on Hansen *et al.*, who used the loss of cells with canopy cover $\geq 50\%$ between 2000 and 2014 to generate the loss data layer. Protected areas in the west and south of Madagascar frequently had low percentages of pixels with canopy cover $\geq 50\%$ due to the natural openness of the forests there (seasonally dry deciduous forest and spiny thicket, respectively). The 50% threshold may thus underestimate total forest loss between 2000 and 2014, but is standardized across the island.

Community Ecology Analyses: Beta Diversity

I calculated the compositional change in diversity between pairs of communities in terms of taxonomic, phylogenetic, and functional beta diversity (TBD, PBD, and FBD, respectively). I calculated pairwise site dissimilarities for taxonomy using the 1-Sorensen's index (*vegdist* function in *vegan*, Oksanen *et al.* 2013), and for the phylogeny using the 1-phylogenetic Sorensen's index (*phylosor* function in *picante*, Kembel *et al.* 2010). 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*, Maechler *et al.* 2015). Filling the missing diet data with data from congeners should not strongly influence the functional distance matrix, and the matrix without imputing missing data was positively related to the matrix with the missing data imputed (Mantel test, $r = 0.84$, $P = 0.001$, $N = 4753$ pairwise comparisons). I calculated the pairwise site dissimilarities using the functional trait dissimilarity matrix using the *pcd* function in *picante*, which standardizes the similarity matrix by species richness (Ives and Helmus 2010).

To determine if protected areas would group together geographically as predicted by the three biogeographic hypotheses based on the lemur phylogenetic beta diversity, I clustered the protected areas based on their phylogenetic beta diversity (similarity indices) using the clustering algorithms in the R package *recluster* (Dapporto *et al.* 2013). I used the function *recluster.boot* to create an unbiased dendrogram (unweighted pair group method with arithmetic mean, UPGMA) that clustered sites based on the phylogenetic similarity of lemur communities (10 trees, resampling the order of the rows of the site \times species matrix for each tree). I assessed the confidence in the UPGMA dendrogram using by bootstrapping the rows of the site \times species matrix 100 times and creating 10 trees for each of bootstrap replicate, each time randomizing the order of the sites in the resampled data, and then deriving the 50% majority consensus tree. This approach gives a hierarchical clustering of sites that is unbiased to the order of the sites, ties, and 0 values in the matrix (Dapporto *et al.* 2013).

To test if allopatric separation explained beta diversity, I partitioned TBD and PBD into turnover and nestedness components, which represent different forms of species

compositional change among communities (Baselga 2010) using the R package betapart (Baselga and Orme 2012). Turnover refers to the composition of species changing from one site to another due to species replacement, while nestedness refers to compositional change due to sites being nested subsets of richer sites. Turnover, especially in PBD, is consistent with allopatric separation of species among sites, while nestedness is consistent with the extirpation of species from a site.

Mantel Tests

To test the predictions of the biogeographic hypotheses on beta diversity related to environment, geography, and river barriers, I tested if TBD, PBD, and FBD correlated with each other and with environmental distance matrices using partial Mantel tests (*mantel* function in *ecodist*, Goslee and Urban 2007). Specifically I was interested in patterns of PBD beyond those predicted given TBD and FBD, so I tested the relationships of environmental distance matrices on PBD, including TBD and FBD as independent matrices. Each environmental predictor dissimilarity matrix was based on Euclidean distances of the z-scores of natural log transformed environmental data. I created eight distance matrices from the subsets of environmental variables: temperature distance, precipitation distance, topographic distance (elevation and SD of elevation), productivity distance (NDVI and net primary productivity), whether protected areas were in the same ecoregion or not (0/1 coding), geographic distance (physical distance among centroids, in km), and the least-cost path distance representing the additional distance among protected areas to circumvent rivers. The geographic distance matrices were calculated based on the distances among centroids of protected areas using the *earth.dist* function in the *fossil* package (Vavrek 2011).

I conducted partial Mantel correlations predicting each beta diversity metric (PBD, TBD, and FBD) from temperature, precipitation, productivity, topographic, geographic, and least-cost path distance matrices, as well as the other beta diversity metrics, i.e., PBD controlling for TBD and FBD). Partial Mantel tests were performed testing the relationship of the y matrix and the $\times 1$ matrix, controlling for $\times 2, \times 3 \dots \times i$ matrices, where i is the number of predictor matrices. The rows and columns of the y matrix were permuted 10,000 times, and the matrix was sampled with 1000 jackknife pseudo-replicates to determine the 95% confidence intervals around the coefficient estimates. To generate the coefficients and confidence intervals for each predictor matrix controlling for the other matrices, I alternated which predictor matrix was first in the regression formula. The two-tailed α value was set at 0.05 for all tests.

Mantel correlations assume linear relationships among distance matrices, which may limit their utility in ecological applications where variables may have nonlinear relationships (Ferrier *et al.* 2007; Legendre *et al.* 2015). I first evaluated if there may be nonlinear relationships in the matrices by plotting Mantel correlograms of each variable plotted against geographic distance, as well as plotting PBD versus all other variables (*mgram* function in *ecodist*). These correlograms revealed that all three lemur beta diversity measures had nonlinear relationships with each other, geographic distance, and environmental predictor matrices (ESM Fig. S4). To account for the nonlinear relationships, I compared models in which the full set of predictor matrices was included, and in which the quadratic term for each predictor matrix was also included. The difference in R^2 between the model with the full set of linear predictors and the

model with the quadratic predictors was taken as the additional variation in PBD explained by nonlinear relationships (Cohen *et al.* 2013).

Alpha Diversity

To investigate the effects of ecological biogeography on the composition of local communities, I quantified taxonomic, phylogenetic, and functional trait alpha diversity in each protected area, with the species lists for each of the five regions as the source pools. At this level, local processes such as interspecies interactions, e.g., competition or mutualisms, and environmental filtering, e.g., resource limitation, are more likely to mitigate species co-occurrences than large scale historical processes such as speciation and extinction (Cavender-Bares *et al.* 2009). The size of the protected area also matters at this scale as it relates to local extirpations, which become more likely with smaller areas (Matthews *et al.* 2014; Sreekar *et al.* 2015).

I calculated taxonomic diversity as the species richness, or total number of species with ranges overlapping the protected area. I calculated phylogenetic and functional community structure using the mean nearest taxon distance (MNTD), which is a measure of the mean pairwise branch-length distance to the closest relative among pairs of co-occurring taxa (Webb 2000). MNTD measures the relative relatedness of closely related species (near the tips of the tree). To apply this metric to the functional traits, the functional trait dissimilarity matrix described for beta diversity was used in place of the phylogenetic distances in calculation of MNTD. I standardized the MNTD values and tested if the observed phylogenetic and functional MNTD differed significantly from two null models: 1) randomized presence/absence matrix maintaining sample species richness (richness null model, in *picante*); and 2) randomized presence/absence maintaining both sample species richness and species prevalence (independent swap null model in *picante*). These two null models were chosen because they were shown to have good statistical properties while representing two different models of null community assembly, the latter accounting for differences in how many sites a species occupies (Kembel and Hubbell 2006). The null models were generated from 999 randomizations of the community data. Negative MNTD values with a probability of meeting the null expectation <0.05 were considered phylogenetically clustered while positive MNTD values with probabilities >0.95 were considered phylogenetically overdispersed ($\alpha_{\text{two-tailed}} = 0.10$). Finally, I calculated the phylogenetic endemism of each protected area (Rosauer *et al.* 2009), which represents the geographic restriction of phylogenetic branch lengths represented in each protected area.

Linear Mixed Models

To test the predictions of the biogeographic hypotheses concerning alpha diversity, I first tested for correlations among the community structure metrics (species richness, phylo- and functional-MNTD, phylogenetic endemism). These metrics partially correlated with each other. Therefore, in addition to testing the effects of environmental variables on each diversity dependent variable separately, I used multivariate multiple regression, testing the effects of fixed factors on the linear combination of the species richness, phylogenetic and functional MNTD, and phylogenetic endemism. I used linear mixed models (lmm) using the *lme* function in the *nlme* package, Pinheiro

et al. 2011) with all variables z -scores transformed to have mean = 0 and standard deviation = 1. In these analyses, geographic region was tested as a grouping factor (random effect), environmental variables were fixed effects, and a geographic distance matrix was included in the error structure to control for spatial autocorrelation using the correlation arguments of the *lme* function. I compared the fit of models of each dependent variable and the linear combination of dependent variables 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). The relative fit of the distance decay matrices compared to the null model was compared using the second-order Akaike information criterion (AICc), and the model with the lowest AICc was selected as the best fit. For all variables and in the downstream lms, including a spherical spatial decay matrix was the best model fit. I confirmed model assumptions were met by verifying that the residuals of the models were normally distributed, that the variance in the residuals was homogeneous, and that the observed quantiles met the theoretical quantiles of a normal distribution (Q–Q plot). To summarize results from multiple models, I used model averaging (Burnham and Anderson 2002) as implemented in the R package AICcmodavg (Mazerolle 2013). I computed the model-averaged correlation coefficients for each variable, as well as their revised unconditional standard errors and 95% confidence intervals, and summarized the results graphically. The models included for averaging were those that contained the variable being averaged, and the complete set of models can be found in ESM Table SIV. Coefficients with 95% confidence intervals that do not overlap 0 signify that the independent variable had a significant effect on the dependent variable.

Results

Beta Diversity

Phylogenetic beta diversity (PBD) increased with increasing taxonomic beta diversity (TBD, Mantel test, $r = 0.61$, $P < 0.001$, $N = 4950$ pairwise comparisons for all beta diversity Mantel tests). Functional beta diversity (FBD) increased with increasing PBD ($r = 0.28$, $P < 0.001$). TBD and PBD are predominantly due to species turnover (99.13% of TBD, 100% of PBD), rather than nestedness (< 1% of TBD, 0% of PBD), suggesting that beta diversity is due to species being replaced by different species from one site to another, rather than sites being nested subsets of richer sites (Baselga 2010). The consensus dendrogram clustering protected areas based on the phylogenetic beta diversity of lemur communities (ESM Fig. S2) suggests that protected areas can be clustered into two main groups: 1) those southwest of the Maevarano River in the northwest region and west of the central highlands but also including sites around the Anosy mountain chain such as Andohahela and the littoral forest fragments in the southeast; and 2) all other protected areas, especially those in the northeast, southeast, and a cluster of northwestern protected areas north of the Maevarano River (but also Bora, just south of the river). The geographic distribution of PBD suggests that the highest PBD exists mostly among protected area pairs within the same biome (ESM Fig. S3a); the protected areas with PBD values above the third quartile of the distribution were mainly *within* the eastern rainforests, western dry forests, or southern arid forest. Protected area pairs with low PBD values tended to

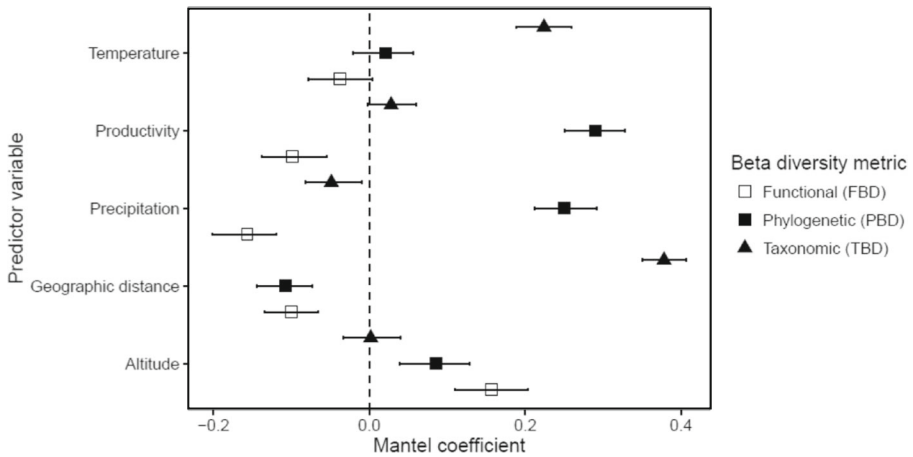


Fig. 3 Effects of environmental variables on three dimensions of lemur beta diversity. The partial Mantel correlation coefficients ($\pm 95\%$ confidence intervals, CI) of the relationships between taxonomic (TBD), phylogenetic (PBD), and functional (FBD) beta diversities with key environmental and geographic gradients. Mantel coefficient probabilities are based on 999 permutations and confidence intervals were calculated based on 999 bootstrap replicates. The vertical dotted line represents no effect.

occur in different biomes (ESM Fig. S3b); protected areas with PBD values below the third quartile occurred *across* the east, south, and west, suggesting similar PBD among protected areas in different biomes.

PBD, TBD, and FBD were significantly related to environmental dissimilarity (Fig. 3). PBD increased with increasing dissimilarity in precipitation ($r = 0.25$, $P = 0.001$) and plant productivity (net primary productivity, $r = 0.29$, $P = 0.001$), after controlling for other environmental variables, TBD and FBD (Fig. 3). PBD was significantly related to whether protected areas were in the same region or not ($r = 0.07$, $P = 0.003$, controlling for other variables), but the least-cost path distance based on rivers as dispersal barriers was not a significant predictor of PBD, controlling for effects of environmental variables and geographic distance ($r = -0.06$, $P = 0.079$).

TBD was most strongly related to temperature and geographic distance (Fig. 3). TBD was significantly associated with whether protected areas were in the same region or not ($r = 0.09$, $P < 0.001$), and TBD increased with increasing least-cost path distance ($r = 0.11$, $P < 0.001$), supporting that communities separated by rivers had significantly different species compositions.

FBD decreased significantly with increasing dissimilarity in precipitation, productivity, and geographic distance (Fig. 3), suggesting protected areas that were geographically close and similar in climate had dissimilar functional diversity. FBD was significantly related to whether protected areas were in the same region or not ($r = 0.15$, $P < 0.001$), but FBD was not significantly related to the least-cost path distance based on rivers as barriers, after controlling for other variables ($r = -0.09$, $P = 0.069$).

There was some evidence for nonlinear relationships among variables (ESM Fig. S4), which led me to investigate quadratic terms in the partial Mantel tests. While there were significant correlations between PBD and the squared distance matrices for productivity ($r = 0.008$, $P = 0.002$), geographic distance ($r = 0.012$, $P = 0.001$),

TBD ($r = 0.27$, $P = 0.001$), and FBD ($r = -0.05$, $P = 0.001$), the variance explained by the Mantel regressions including both linear and quadratic terms increased by only 2.5% over the model with only linear terms ($R^2 = 0.75$). Based on these results, although there are some nonlinear trends, they explain a relatively small proportion of the variance in phylogenetic beta diversity compared to the linear effects.

Alpha Diversity

The phylogenetic relatedness of species within protected areas was overdispersed (33% and 38% for the mean pairwise distance, MPD, and mean nearest taxon distance, MNTD, respectively) or not significantly different from the null expectation (67% and 62%, for MPD and MNTD, ESM Table SIII). The proportion of protected areas that exhibited phylogenetic overdispersion varied significantly among regions: 60% in northeastern wet forests, ca. 40% of the northwestern dry forests and southeastern wet forests 25% of central highland sites, and none of the 25 southwestern dry forest communities (based on MNTD values with $P > 0.95$, $\chi^2 = 26.00$, $df = 4$, $P < 0.001$, $N = 100$). The prevalence of overdispersion in the northeast coincides with the combination of greater forest cover, higher productivity, and higher topographic heterogeneity in that region compared to the others (MANOVA, $F = 8.93$, Pillai's trace = 1.08, $P < 0.001$). The functional similarity of species within 88% of protected areas was not significantly different from the null expectation, while 12% of protected areas were functionally overdispersed (ESM Table SIII). The paucity of functionally overdispersed communities may indicate that most communities have ecologically similar species. Phylogenetic diversity increased with increasing species richness ($t_{94} = 5.25$, $P < 0.001$, $R^2 = 0.22$), but was not related to functional diversity ($t_{94} = -0.65$, $P = 0.520$, $R^2 = < 0.01$). Functional diversity was not related to species richness ($t_{94} = 0.15$, $P = 0.880$, $R^2 < 0.01$), suggesting higher species richness is associated with functional redundancy. Phylogenetic endemism increased with increasing species richness ($t_{94} = 17.34$, $P < 0.001$, $R^2 = 0.59$), suggesting that communities with higher taxonomic richness are likely to have species which represent geographically restricted phylogenetic history than communities with lower taxonomic richness.

The multivariate multiple regression results suggest that the protected area productivity and topographic heterogeneity are the best predictors of the combination of taxonomic, phylogenetic, and functional diversity and phylogenetic endemism (ESM Table SIV). The common drivers of phylogenetic and taxonomic diversity, as well as phylogenetic endemism, were positive relationships with plant productivity, topographic heterogeneity, forest cover, and area; as these environmental variables increased, phylogenetic and taxonomic diversity and phylogenetic endemism increased (Fig. 4, ESM Table SIV). The mean and standard deviation of elevation had an interaction effect on taxonomic diversity, such that at low levels of topographic heterogeneity, elevation had a small effect on diversity, while at higher levels of heterogeneity, diversity increased with increasing elevation (ESM Fig. S5). The common effect of area on diversity and endemism indicates that larger areas support greater taxonomic richness and phylogenetic history. Unlike other measures of community

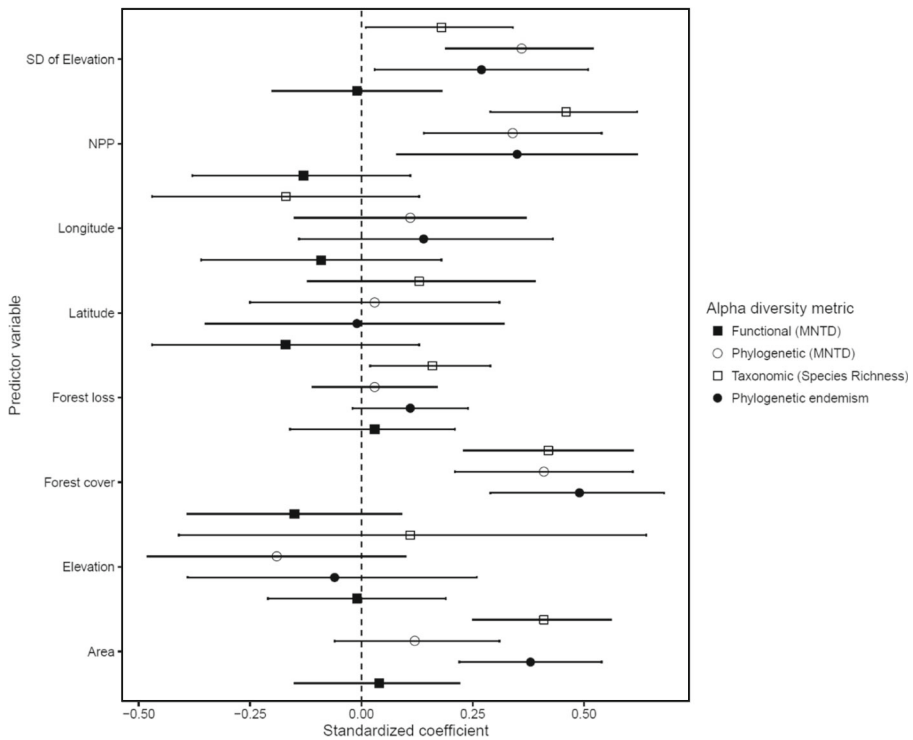


Fig. 4 Effects of environmental and geographic variables on lemur alpha diversity. The model-averaged correlation coefficients and 95% confidence intervals (CI) between diversity metrics and environmental variables.

diversity, functional diversity was not strongly related to any environmental variables (Fig. 4, ESM Table [SIV](#)).

Threats to Community Diversity

Species richness and phylogenetic endemism were positively associated with the area of the protected area (species richness: $t_{93} = 6.27$, $P < 0.001$, $R^2 = 0.24$, phylogenetic endemism: $t_{93} = 6.22$, $P < 0.001$, $R^2 = 0.21$, $N = 100$). The percentage of closed-canopy forest ($\geq 50\%$ canopy closure) in protected areas in the year 2000 was positively related to species richness ($t_{93} = 4.17$, $P < 0.001$, $R^2 = 0.20$), reflecting the importance of large areas of contiguous, closed-canopy forest for supporting high lemur diversity (Fig. 4). Since the year 2000, however, the mean forest loss in protected areas was 4.51%, with up to 31.75% of closed-canopy forest transformed to nonforest in protected areas (ESM Table [SV](#)). In total, closed-canopy forest cover decreased by ca. 3000 km² in protected areas (ESM Table [SVI](#)). The percentage of forest loss was positively related to species richness ($t_{93} = 2.24$, $P = 0.029$), revealing that the highest forest loss occurred in protected areas with the highest species richness and the most forest to lose (Fig. 4, ESM Table [SIV](#)).

Data Availability

Data Accessibility Statement The data reported in this study have been deposited with the *International Journal of Primatology* as online supplementary material, available at <http://dx.doi.org/10.1007/s10764-017-9974-9>.

Discussion

I found that differences in the species and phylogenetic composition of communities were explained by differences in plant productivity, and community diversity was positively related to plant productivity, supporting resource abundance as a limiting factor. Topographic heterogeneity was an important predictor of diversity within communities, supporting the role of elevational gradients in harboring diversity. The results showed that taxonomic and functional dissimilarities among protected areas are independently affected most by the climate and geographic proximity, and phylogenetic dissimilarity was most strongly affected by plant productivity. In addition to the environment, proxies of river barriers were also associated with taxonomic diversity. The results therefore most strongly support the riverine barrier hypothesis, in which both ecological differences among regions and river barriers shaped lemur biogeographic evolution.

Biogeography in Madagascar

The biogeographic hypotheses for speciation mechanisms in Madagascar center on the roles of environmental gradients, riverine dispersal barriers, and Quaternary climate change. Patterns of some species' distributions correspond to different climate niches, suggesting ecological adaptation driving species differentiation (Blair *et al.* 2013; Kamilar and Muldoon 2010; Muldoon and Goodman 2010; Pearson and Raxworthy 2009). Within ecoregions, key rivers have also limited dispersal for some species based on phylogeography (Martin 1972; Pastorini *et al.* 2003). Microendemic species appear to have ranges restricted to watersheds of rivers at low elevations (Mercier and Wilmé 2013; Wilmé *et al.* 2006). In addition, there are distinct mountain chains that have been hypothesized to generate diversity because heterogeneous environments provide opportunities for niche partitioning (Wollenberg *et al.* 2008). The phylogenetic structure of lemur diversity observed in this study supports the roles of both contrasting climates and geographic isolation across the island leading to ecological and allopatric divergence. This result confirms the necessarily pluralistic understanding of the biogeographic evolution on Madagascar (Brown *et al.* 2014; Pearson and Raxworthy 2009).

My results support the riverine barrier hypothesis, which posits that both ecological gradients and river dispersal barriers shaped lemur biogeography. I found that increasing differences in phylogenetic, taxonomic, and functional beta diversity were associated with increasing differences in climate and plant productivity, and whether protected areas were in the same ecoregion or not. Greater geographic distances among protected areas were related to greater differences in species composition and lower phylogenetic turnover. Beta diversity was largely due to species turnover, rather than

nestedness, suggesting that allopatric separation of species is the main cause of species compositional differences, rather than local extirpations of extant species from communities. While variation in all three measures of beta diversity was significantly explained by whether the protected areas were in the same ecoregion or not, the least-cost path distances among protected areas based on rivers as barriers was not significantly related to phylogenetic beta diversity, but was positively associated with taxonomic beta diversity. The clustering analysis based on phylogenetic beta diversity suggested that protected areas southwest of the Maevarano river (except Bora), west of the highlands, and around the Anosy mountains in the southeast grouped together, while the sites north of the Maevarano, through the central highlands and along the east form a group. The negative relationship between phylogenetic beta diversity and geographic distance among protected areas suggests deeply divergent endemic lineages among geographically close protected areas. The protected areas with the highest phylogenetic beta diversity occurred within the east and west, and low phylogenetic beta diversity was observed among protected areas in different ecoregions (between protected areas of the wet east and dry west). This result lends support to the hypothesis that the central highlands were not barriers to dispersal in the past; instead, the highlands may have facilitated longitudinal dispersal due to riparian conditions along rivers that span the east and west (Ganzhorn *et al.* 2006; Yoder *et al.* 2016). Thus, rivers likely had an influence on lemur biogeographic evolution, with some possibly acting as dispersal barriers, while others may have been dispersal corridors among ecoregions.

While the results support the influence of ecoregions on lemur diversity, they also point to the more proximal mechanisms of differentiation – differences in productivity and topographic heterogeneity among regions. While climate variables were associated with diversity measures, increasing phylogenetic beta diversity was best explained by increasing dissimilarity in plant productivity; protected areas with low productivity shared similar, depauperate lemur communities that were phylogenetically and taxonomically different from the diverse communities with high productivity. The most taxonomically and phylogenetically diverse communities occurred in localities with the highest net primary productivity, clearly illustrating the coupling of primary production and secondary consumer diversity. I measured productivity from remotely sensed data on the absorbed photosynthetically active radiation, which is a useful proxy for biomass production (Gower *et al.* 1999; Zhao *et al.* 2014). The results are congruent with the finding that dry forests had lower species richness than wet forests, related to a similar pattern in tree species richness (Ganzhorn *et al.* 1997). Topographic heterogeneity, which was highest in the eastern rainforest, was also an important predictor of diversity within communities, supporting the concept that montane regions promote diversity by harboring many opportunities for niche partitioning and isolation, as found for Malagasy cophyline frogs (Wollenberg *et al.* 2008) and for North American mammals (Kerr and Packer 1997). Lemurs of the eastern rainforest tend to have wider elevational distributions than Neotropical or Asian primates, leading to higher species richness in Malagasy communities on mountains than in South America or Asia (Goodman and Ganzhorn 2004b), which may be explained by the positive association between elevation, the standard deviation of elevation, and species richness observed in this study. Variation in lemur species' elevational distributions may explain variation in species' dispersal abilities and thus their total geographic range, with species that are restricted to lower elevations being more likely to be dispersal limited than species

which range to higher elevations above riverine barriers (Goodman and Ganzhorn 2004a). The combined effects of low productivity and low topographic heterogeneity in western Madagascar is therefore important in explaining the lower lemur diversity in the west than the east. Functional diversity was not strongly related to environmental factors or phylogenetic diversity, rejecting competitive exclusion as a primary mechanism of community assembly. Further investigation is required to determine if resource limitation influences functionally important traits not examined in this study.

Previous studies have suggested rivers may not be dispersal barriers for lemurs (Craul *et al.* 2008; Goodman and Ganzhorn 2004a; Muldoon and Goodman 2015). In contrast, I found that protected areas within the same ecoregions but separated by rivers had higher phylogenetic beta diversity than expected given geographic distance, indicating communities separated by rivers are composed of relatively ancient lineages. Further, taxonomic beta diversity was higher with greater distances among protected areas due to rivers, supporting the role of rivers in structuring community assembly. River barriers are prominent causes of patterns in diversity, e.g., Amazon (Boubli *et al.* 2015), Congo (Voelker *et al.* 2013), and Mekong (Geissler *et al.* 2015), preventing interbreeding among segregated populations and leading to speciation, as well as reducing colonization. Similarly, large rivers within ecoregions in Madagascar may have played an important role in lemur biogeographic history. The role of rivers in structuring communities is further supported by the prevalence of phylogenetic overdispersion in alpha diversity with low functional diversity, suggesting allopatric speciation as a cause of phylogenetic overdispersion.

Phylogenetic and functional alpha diversity are frequently assumed to be positively related, but recently this assumption has been questioned (Mayfield *et al.* 2010). In this study, taxonomic and phylogenetic diversity were not positively related to functional diversity. Instead, the protected areas with the highest species richness had low functional diversity, suggesting that communities consist of functionally redundant species. In contrast, in the southern arid forests of Madagascar, species richness is low while functional diversity is high. This may be an indication of competition driving trait divergence among sympatric species. Indeed the southern arid protected areas had the lowest productivity, and I interpret the high functional diversity as evidence of niche partitioning where resources are limited. Where resources are abundant, such as the high-productivity eastern rainforests, species have functionally redundant traits. Further research is needed, however, to quantify other functionally relevant traits not measured in this study, such as the chemical composition of preferred foods and the vertical forest stratum used by different species. These traits have also been found to relate to niche partitioning in lemurs (Ganzhorn 1988), and should be evaluated in future studies.

Effects of Forest Loss and Conservation Implications

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 phylogenetic diversity is generally found in the east, but I also identified exceptions that warrant special attention, e.g., in the northwest. Species richness and phylogenetic endemism both increased with increasing geographic area of the protected area, supporting the

importance of large areas for supporting high diversity. These high-diversity protected areas are under heavy threat from anthropogenic habitat loss. The percentage of deforestation in protected areas was high, up to 31%, and immediate action is needed to prevent the loss of diversity and species extinctions in this highly threatened mammalian group. Declines in diversity are linked to eroding ecosystem function and resilience (Oliver *et al.* 2015), and here I have shown how the communities with the highest diversity have been greatly degraded since the turn of the century. It is imperative to mobilize conservation efforts toward greater protection for areas with the highest combination of diversity and forest loss to preserve the multiple dimensions of unparalleled biodiversity and prevent further declines in ecosystem quality.

Further research should be conducted using the framework presented here for other taxonomic groups, because differences in traits and dispersal ability among organismal groups will elucidate the causes of plurality in community ecology and biogeographic evolution. 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.

Acknowledgements I thank the National Science Foundation (Graduate Research Fellowship), Stony Brook University (Turner Fellowship), and the American Museum of Natural History (Gerstner Scholarship) for funding. I thank the following colleagues for helpful comments on this research and earlier drafts of the manuscript: P. C. Wright, E. R. Seiffert, L. M. Dávalos, W. L. Jungers, C. L. Nunn, C. H. Graham, C. Raxworthy, J. J. Flynn, N. B. Simmons, W. Pearse, and S. Desbureaux; members of the AMNH Ecological and Evolutionary Modelling Discussion Group, especially F. Burbrink; and members of the AMNH Center for Biodiversity and Conservation, especially S. Macey. I thank three anonymous reviewers of this manuscript submitted elsewhere, two anonymous reviewers at *International Journal of Primatology*, and especially J. Setchell for giving helpful feedback on earlier versions of this manuscript and pointing out ways to improve the research.

References

- Bannar-Martin, K. H. (2014). Primate and nonprimate mammal community assembly: the influence of biogeographic barriers and spatial scale. *International Journal of Primatology*, 35(6), 1122–1142.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143.
- Baselga, A., & Orme, C. D. L. (2012). Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812.
- Beaudrot, L. H., & Marshall, A. J. (2011). Primate communities are structured more by dispersal limitation than by niches. *Journal of Animal Ecology*, 80(2), 332–341.
- Blair, M., Sterling, E., Dusch, M., Raxworthy, C., & Pearson, R. (2013). Ecological divergence and speciation between lemur (*Eulemur*) sister species in Madagascar. *Journal of Evolutionary Biology*, 26(8), 1790–1801.
- Boubli, J. P., Ribas, C., Alfaro, J. W. L., Alfaro, M. E., da Silva, M. N. F., et al (2015). Spatial and temporal patterns of diversification on the Amazon: a test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. *Molecular Phylogenetics and Evolution*, 82, 400–412.
- Brook, G. A., Raftter, M. A., Railsback, L. B., Sheen, S.-W., & Lundberg, J. (1999). A high-resolution proxy record of rainfall and ENSO since AD 1550 from layering in stalagmites from Anjohibe cave, Madagascar. *The Holocene*, 9(6), 695–705.
- Brown, J. L., Cameron, A., Yoder, A. D., & Vences, M. (2014). A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature Communications*, 5, 5046.
- Brunsdon, C., & Chen, H. (2014). GISTools: some further GIS capabilities for R: CRAN. <https://CRAN.R-project.org/package=GISTools>

- Burney, D. A., Burney, L. P., Godfrey, L. R., Jungers, W. L., Goodman, S. M., et al (2004). A chronology for late prehistoric Madagascar. *Journal of Human Evolution*, 47(1), 25–63.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science+Business Media.
- Burns, S. J., Godfrey, L. R., Faina, P., McGee, D., Hardt, B., et al (2016). Rapid human-induced landscape transformation in Madagascar at the end of the first millennium of the common era. *Quaternary Science Reviews*, 134, 92–99.
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7), 693–715.
- Cohen, J., Cohen, P., West, S. G., & Aiken, L. S. (2013). *Applied multiple regression/correlation analysis for the behavioral sciences*. New York: Routledge.
- Craul, M., Radespiel, U., Rasolofson, D., Rakotondratsimba, G., Rakotonirainy, O., et al (2008). Large rivers do not always act as species barriers for *Lepilemur* sp. *Primates*, 49(3), 211–218.
- Crowley, B. E., Godfrey, L. R., Bankoff, R. J., Perry, G. H., Culleton, B. J., et al (2016). Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. *Ecography*. doi:10.1111/ecog.02376.
- Dapporto, L., Ramazzotti, M., Fattorini, S., Talavera, G., Vila, R., & Dennis, R. L. (2013). Recluster: an unbiased clustering procedure for beta-diversity turnover. *Ecography*, 36(10), 1070–1075.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, 13(8), 1030–1040.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61(1), 1–10.
- Fernani, P. N., & Ruggiero, A. (2015). Ecological diversity in south American mammals: their geographical distribution shows variable associations with phylogenetic diversity and does not follow the latitudinal richness gradient. *PloS One*, 10(6), e0128264.
- Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, 13(3), 252–264.
- Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia*, 75(3), 436–450.
- Ganzhorn, J. (1997). Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. *Journal of Zoology*, 241(3), 533–542.
- Ganzhorn, J. U., Malcomber, S., Adrianantoanina, O., & Goodman, S. M. (1997). Habitat characteristics and lemur species richness in Madagascar. *Biotropica*, 29, 331–343.
- Ganzhorn, J. U., Wright, P. C., & Ratsimbazafy, J. (1999). Primate communities: Madagascar. In J. Fleagle, C. Janson, & K. Reed (Eds.), *Primate communities* (pp. 75–89). Cambridge: Cambridge University Press.
- Ganzhorn, J. U., Goodman, S. M., Nash, S., & Thalmann, U. (2006). Lemur biogeography. In J. G. Fleagle & S. M. Lehman (Eds.), *Primate biogeography: progress and perspectives* (pp. 229–254). Developments in Primatology: Progress and Prospects. New York: Springer Science+Business Media.
- Geissler, P., Hartmann, T., Ihlow, F., Rödder, D., Poyarkov, N. A., et al (2015). The lower Mekong: an insurmountable barrier to amphibians in southern Indochina? *Biological Journal of the Linnean Society*, 114(4), 905–914.
- Godfrey, L. R., Jungers, W. L., & Burney, D. A. (2010). Subfossil lemurs of Madagascar. In L. Werdelin & W. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 351–367). Berkeley: University of California Press.
- Goodman, S. M., & Ganzhorn, J. U. (2004a). Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *Journal of Biogeography*, 31(1), 47–55.
- Goodman, S. M., & Ganzhorn, J. U. (2004b). Elevational ranges of lemurs in the humid forests of Madagascar. *International Journal of Primatology*, 25(2), 331–350.
- Goodman, S. M., & Jungers, W. L. (2014). *Extinct Madagascar: picturing the island's past*. Chicago: University of Chicago Press.
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22(7), 1–19.
- Gower, S. T., Kucharik, C. J., & Norman, J. M. (1999). Direct and indirect estimation of leaf area index, f APAR, and net primary production of terrestrial ecosystems. *Remote Sensing of Environment*, 70(1), 29–51.
- Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecology Letters*, 11(12), 1265–1277.
- Graham, C. H., & Hijmans, R. J. (2006). A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, 15(6), 578–587.

- Groeneveld, L., Weisrock, D., Rasoloarison, R., Yoder, A., & Kappeler, P. (2009). Species delimitation in lemurs: multiple genetic loci reveal low levels of species diversity in the genus *Cheirogaleus*. *BMC Evolutionary Biology*, 9(1), 30.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S., et al (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853.
- Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34(4), 325–333.
- Heinsch, F. A., Reeves, M., Votava, P., Kang, S., Milesi, C., et al. (2003). GPP and NPP (MOD17A2/A3) products NASA MODIS land algorithm. *MOD17 User's Guide*, 1–57.
- Helmus, M. R., Savage, K., Diebel, M. W., Maxted, J. T., & Ives, A. R. (2007). Separating the determinants of phylogenetic community structure. *Ecology Letters*, 10(10), 917–925.
- Herrera, J. P., & Dávalos, L. (2016). Phylogeny and divergence times of lemurs inferred with recent and ancient fossils in the tree. *Systematic Biology*, 65(5), 772–791.
- Hijmans, R. J. (2015). Raster: Geographic data analysis and modeling. CRAN. <http://cran.r-project.org/web/packages/raster/index.html>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978.
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the USA*, 104(33), 13384–13389.
- Ives, A. R., & Helmus, M. R. (2010). Phylogenetic metrics of community similarity. *The American Naturalist*, 176(5), E128–E142.
- Kamilar, J. M. (2009). Environmental and geographic correlates of the taxonomic structure of primate communities. *American Journal of Physical Anthropology*, 139(3), 382–393.
- Kamilar, J. M., & Guidi, L. M. (2010). The phylogenetic structure of primate communities: variation within and across continents. *Journal of Biogeography*, 37(5), 801–813.
- Kamilar, J. M., & Muldoon, K. M. (2010). The climatic niche diversity of Malagasy primates: a phylogenetic perspective. *PloS One*, 5(6), e11073.
- Karpanty, S. M., & Wright, P. C. (2007). Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In *Primate anti-predator strategies* (pp. 77–99). Developments in primatology: progress and prospects. New York: Springer Science+Business Media.
- Kemmel, S. W., & Hubbell, S. P. (2006). The phylogenetic structure of a neotropical forest tree community. *Ecology*, 87(7), S86–S99.
- Kemmel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., et al (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463–1464.
- Kerr, J. T., & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385(6613), 252–254.
- Koechlin, J. (1972). Flora and vegetation of Madagascar. In *Biogeography and ecology in Madagascar* (pp. 145–190). New York: Springer-Verlag.
- Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., et al (2008). Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, 320(5873), 222–226.
- Legendre, P., Fortin, M. J., & Borcard, D. (2015). Should the mantel test be used in spatial analysis? *Methods in Ecology and Evolution*, 6(11), 1239–1247.
- Lei, R., Engberg, S. E., Andriantompohavana, R., McGuire, S. M., Mittermeier, R. A., et al (2008). Nocturnal lemur diversity at Masoala National Park. *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*. Lubbock: Museum of Texas Tech University.
- Louis, E. E., & Lei, R. (2016). Mitogenomics of the family Cheirogaleidae and relationships to taxonomy and biogeography in Madagascar. In S. M. Lehman, U. Radespiel, & E. Zimmermann (Eds.), *The dwarf and mouse lemurs of Madagascar: biology, behavior, and conservation biogeography of the Cheirogaleidae*. London: Cambridge University Press.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., Studer, M., & Roudier, P. (2015). Cluster analysis extended Rousseeuw et al. CRAN. <http://cran.r-project.org/web/packages/cluster/index.html>
- Markolf, M., Brameier, M., & Kappeler, P. (2011). On species delimitation: yet another lemur species or just genetic variation? *BMC Evolutionary Biology*, 11, 216.
- Markolf, M., Rakotonirina, H., Fichtel, C., von Grumbkow, P., Brameier, M., & Kappeler, P. M. (2013). True lemurs ... true species-species delimitation using multiple data sources in the brown lemur complex. *BMC Evolutionary Biology*, 13(1), 233.

- Martin, R. D. (1972). Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 264, 295–352.
- Matthews, T. J., Cottee-Jones, H. E., & Whittaker, R. J. (2014). Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, 20(10), 1136–1146.
- Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13(9), 1085–1093.
- Mazerolle, M. (2013). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). v1.28. CRAN. <https://CRAN.R-project.org/package=AICcmodavg>
- Mercier, J.-L., & Wilmé, L. (2013). The eco-geo-Clim model: explaining Madagascar's endemism. *Madagascar Conservation & Development*, 8(2), 63–68.
- Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, 30(5), 241–247.
- Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., et al (2010). *Lemurs of Madagascar* (3rd ed.). Washington, DC: Conservation International.
- Muldoon, K. M., & Goodman, S. M. (2010). Ecological biogeography of Malagasy non volant mammals: community structure is correlated with habitat. *Journal of Biogeography*, 37(6), 1144–1159.
- Muldoon, K. M., & Goodman, S. M. (2015). Primates as predictors of mammal community diversity in the forest ecosystems of Madagascar. *PloS One*, 10(9), e0136787.
- Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., et al (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545), 45–50.
- Ohba, M., Samonds, K. E., LaFleur, M., Ali, J. R., & Godfrey, L. R. (2016). Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441, 688–695.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., et al. (2013). Package 'vegan.' CRAN. <https://CRAN.R-project.org/package=vegan>
- Oliver, T. H., Isaac, N. J., August, T. A., Woodcock, B. A., Roy, D. B., & Bullock, J. M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, 6, 10122.
- Ossi, K., & Kamilar, J. M. (2006). Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (primates: Lemnidae). *Behavioral Ecology and Sociobiology*, 61(1), 53–64.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analysis of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Pastorini, J., Thalmann, U., & Martin, R. D. (2003). A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences of the USA*, 100(10), 5879–5884.
- Pearson, R. G., & Raxworthy, C. J. (2009). The evolution of local endemism in Madagascar: watershed versus climatic gradient hypotheses evaluated by null biogeographic models. *Evolution*, 63(4), 959–967.
- Perez, V. R., Godfrey, L. R., Nowak-Kemp, M., Burney, D. A., Ratsimbazafy, J., & Vasey, N. (2005). Evidence of early butchery of giant lemurs in Madagascar. *Journal of Human Evolution*, 49(6), 722–742.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2011). Nlme: linear and nonlinear mixed effects models. R package version 3.1–97. CRAN. <https://CRAN.R-project.org/package=nlme>
- Price, T. D., Hooper, D. M., Buchanan, C. D., Johansson, U. S., Tietze, D. T., et al (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509(7499), 222–225.
- Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405(6783), 212–219.
- Quantum GIS Development Team. (2015). Quantum GIS geographic information system. Open Source Geospatial Foundation Project. <http://www.qgis.org/en/site/>
- R Core Team. (2014). R: a language and environment for statistical computing. <http://www.R-project.org/>.
- Radespiel, U., Ratsimbazafy, J., Rasoloharijaona, S., Raveloson, H., Andriaholinirina, N., Rakotondravony, R., Randrianarison, R., & Randrianambinina, B. (2011). First indications of a highland specialist among mouse lemurs (*Microcebus* spp.) and evidence for a new mouse lemur species from eastern Madagascar. *Primates*, 53(2), 157–170.
- Rangel, T. F., Colwell, R. K., Graves, G. R., Fučíková, K., Rahbek, C., & Diniz-Filho, J. A. F. (2015). Phylogenetic uncertainty revisited: Implications for ecological analyses. *Evolution*. doi:10.1111/evo.12644.
- Rasoloarison, R. M., Weisrock, D. W., Yoder, A. D., Rakotondravony, D., & Kappeler, P. M. (2013). Two new species of mouse lemurs (Cheirogaleidae: *Microcebus*) from eastern Madagascar. *International Journal of Primatology*, 34(3), 455–469.
- Razafindratsima, O. H., Mehtani, S., & Dunham, A. E. (2013). Extinctions, traits and phylogenetic community structure: insights from primate assemblages in Madagascar. *Ecography*, 36(1), 47–56.

- Razafindratsima, O. H., Jones, T. A., & Dunham, A. E. (2014). Patterns of movement and seed dispersal by three lemur species. *American Journal of Primatology*, 76(1), 84–96.
- Rosauer, D., Laffan, S. W., Crisp, M. D., Donnellan, S. C., & Cook, L. G. (2009). Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, 18(19), 4061–4072.
- Samonds, K. E., Godfrey, L. R., Ali, J. R., Goodman, S. M., Vences, M., et al (2013). Imperfect isolation: factors and filters shaping Madagascar's extant vertebrate fauna. *PloS One*, 8(4), e62086.
- Scales, I. R. (2014). The drivers of deforestation and the complexity of land use in Madagascar. In I. Scales (Ed.), *Conservation and environmental management in Madagascar* (pp. 105–125). New York: Routledge.
- Schwitzer, C., Mittermeier, R., Johnson, S. E., Donati, G., Irwin, M. T., et al (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343, 842–843.
- Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of Human Evolution*, 32(6), 523–559.
- Smith, B. T., McCormack, J. E., Cuervo, A. M., Hickerson, M. J., Aleixo, A., et al (2014). The drivers of tropical speciation. *Nature*, 515(7527), 406–409.
- Sreekar, R., Huang, G., Zhao, J. B., Pasion, B. O., Yasuda, M., et al (2015). The use of species–area relationships to partition the effects of hunting and deforestation on bird extirpations in a fragmented landscape. *Diversity and Distributions*, 21(4), 441–450.
- Swenson, N. G., Enquist, B. J., Pither, J., Thompson, J., & Zimmerman, J. K. (2006). The problem and promise of scale dependency in community phylogenetics. *Ecology*, 87(10), 2418–2424.
- Tattersall, I. (2007). Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evolutionary Anthropology*, 16, 12–23.
- van Etten, J. (2012). Gdistance: distances and routes on geographical grids. CRAN. <https://CRAN.R-project.org/package=gdistance>
- Vavrek, M. J. (2011). Fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica*, 14(1), 16.
- Vences, M., Wollenberg, K. C., Vieites, D. R., & Lees, D. C. (2009). Madagascar as a model region of species diversification. *Trends in Ecology & Evolution*, 24(8), 456–465.
- Virah-Sawmy, M., Willis, K. J., & Gillson, L. (2010). Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. *Journal of Biogeography*, 37(3), 506–519.
- Voarintsoa, N. R. G., Wang, L., Railsback, L. B., Brook, G. A., Liang, F., et al. (2017). Multiple proxy analyses of a U/Th-dated stalagmite to reconstruct paleoenvironmental changes in northwestern Madagascar between 370CE and 1300CE. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 469, 138–155.
- Voelker, G., Marks, B., Kahindo, C., A'genonga, U., Bapeamoni, F., et al (2013). River barriers and cryptic biodiversity in an evolutionary museum. *Ecology and Evolution*, 3(3), 536–545.
- Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist*, 156, 145–155.
- Wilmé, L., Goodman, S. M., & Ganzhorn, J. U. (2006). Biogeographic evolution of Madagascar's microendemic biota. *Science*, 312(5776), 1063–1065.
- Wollenberg, K. C., Vieites, D. R., Van Der Meijden, A., Glaw, F., Cannatella, D. C., & Vences, M. (2008). Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. *Evolution*, 62(8), 1890–1907.
- Wright, P. C., & Martin, L. B. (1995). Predation, pollination, and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rainforest of Madagascar. In L. Alterman, G. Doyle, & K. Izard (Eds.), *Creatures of the dark: the nocturnal prosimians* (pp. 45–60). New York: Springer-Verlag.
- Yoder, A. D., Olson, L. E., Hanley, C., Heckman, K. L., Rasoloarison, R., et al (2005). A multidimensional approach for detecting species patterns in Malagasy vertebrates. *Proceedings of the National Academy of Sciences of the USA*, 102(supplement 1), 6587–6594.
- Yoder, A. D., Campbell, C. R., Blanco, M. B., dos Reis, M., Ganzhorn, J. U., et al. (2016). Geogenetic patterns in mouse lemurs (genus *Microcebus*) reveal the ghosts of Madagascar's forests past. *Proceedings of the National Academy of Sciences of the USA*, 201601081.
- Zhao, F., Xu, B., Yang, X., Jin, Y., Li, J., et al (2014). Remote sensing estimates of grassland aboveground biomass based on MODIS net primary productivity (NPP): a case study in the Xilingol grassland of northern China. *Remote Sensing*, 6(6), 5368–5386.