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Primate and Nonprimate Mammal Community Assembly: The Influence of Biogeographic Barriers and Spatial Scale

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Abstract At least three community assembly processes shape communities: 1) environmental niche-based processes, 2) spatial effects through dispersal limitation, and 3) biogeographic dispersal barriers. Previous studies suggested primate communities were dispersal limited, except in Madagascar, where environmental effects shaped communities. However, previous work did not investigate the role of biogeographic barriers. Further, the relative roles of these processes are potentially specific to taxonomic and/or functional groups owing to a group's ecological preferences. I aimed to identify to what extent environmental factors, spatial effects, and biogeographic barriers shape patterns of primate and nonprimate community composition, in comparison to terrestrial and arboreal mammal communities in Madagascar. I analyzed occurrence data of nonvolant mammals and site-specific environmental and biogeographic data for 34 sites in Madagascar using principal coordinates of neighbor matrices and variation partitioning to test the relative contribution of environmental, spatial, and biogeographic effects to the patterns of community composition. Environmental and spatial effects almost equally explained nonvolant mammal communities. However, for primate and arboreal mammal communities, especially at broad spatial scales, spatial effects explained more of the variation than environmental effects. By contrast, only environmental effects explained nonprimate and terrestrial mammal distributions. Biogeographic effects were not significant for any community type. The difference between arboreal and terrestrial mammals is perhaps due to functional differences in dispersal ability, which habitat modification and a large impassable agricultural matrix in Madagascar may compound. Future research should consider the influence of functional diversity on patterns of community assembly.

Keywords Biogeography · Community assembly · Dispersal · Functional group · Scale

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Introduction

Ecological communities form through a complex interplay of community assembly processes (Chase and Myers 2011; Diamond 1975). At least three processes have been separately hypothesized to influence the formation of ecological communities, which are broadly categorized as deterministic (niche differentiation, environmental effects; Chase and Leibold 2003; Chase and Myers 2011), stochastic (spatial effects, neutral theory, dispersal limitation by distance, mid-domain effect, environmental stochasticity, demographic stochasticity; Colwell and Lees 2000; Hubbell 2001; Lees *et al.* 1999; MacArthur and Wilson 1967; Tokeshi 1999), and biogeographic processes (historical process, evolutionary process, biogeographic barriers; Simpson 1953; Tokeshi 1999; Vences *et al.* 2009). Most of this research examined organisms other than primates (Cottenie 2005; cf. Beaudrot and Marshall 2011; Beaudrot *et al.* 2014; Gavilanez and Stevens 2013; Kamilar 2009). The extent to which each of these processes contributes to the formation of ecological communities, however, varies by clade and geographic region (Condit *et al.* 2002; Qian and Ricklefs 2012). Although processes operate in a nonmutually exclusive framework (Chase and Myers 2011; Gravel *et al.* 2006; Leibold and McPeck 2006), identifying and comparing components and contributions of each process to community assembly will further understanding of environmental and spatial influences on community structure (Chase and Myers 2011; Gravel *et al.* 2006; Leibold and McPeck 2006).

Previous studies of deterministic and stochastic processes have been predominantly focused on the roles of environmental effects and dispersal limitation in shaping community assembly (Beaudrot and Marshall 2011; Lindo and Winchester 2009; Morris 2005). The role that biogeographic dispersal barriers, or vicariance events, have played in shaping community assembly has gone largely unexplored (cf. Gavilanez and Stevens 2013), despite the importance of historical biogeographic barriers in community assembly (Condit *et al.* 2002; Ricklefs 1987; Tuomisto *et al.* 2003). Studies have shown that biogeographic barriers can shape patterns of mammal diversity (Brown 1978; Harcourt and Wood 2012; Lomolino and Davis 1997) and patterns of endemism in Madagascar (Pastorini *et al.* 2003; Pearson and Raxworthy 2009; Wilmé *et al.* 2006). For example, rivers serve as boundaries or refugia for some nonvolant mammals in Madagascar (Ganzhorn *et al.* 2006; Goodman and Ganzhorn 2004b; Pastorini *et al.* 2003; Pearson and Raxworthy 2009; Wilmé *et al.* 2006). In addition, mountain ranges and elevation changes can act as biogeographic barriers to mammal distributions (Cortes-Ortiz *et al.* 2003; Goodman and Ganzhorn 2004a). Patterns of extant community composition can also be the result of speciation generating different species assemblages. In Madagascar these include speciation events shaped by ecogeographic constraints, western rainforest refugia, riverine barriers, montane refugia, and watershed positions, which are all shaped by past climate shifts (Vences *et al.* 2009).

The composition and diversity of communities are also structured by processes that operate at a variety of spatial scales (Borcard *et al.* 2004; Chase and Myers 2011; Leibold *et al.* 2004; Wiens 1989). Regional diversity patterns are the result of local processes, underlying environmental heterogeneity, and species dispersal (Ricklefs and Schluter 1993), and at larger spatial scales differences in geographic ranges, biological

regions (Morris 2005), and the prevalence of biogeographic barriers (cf. Lomolino and Davis 1997). At the local scale interactions and niche-based processes (competition and direct interactions) operate (cf. Harrison and Cornell 2008). However, interspecific competition can also influence large-scale variation in species co-occurrence patterns (Beaudrot and Marshall 2011; Beaudrot *et al.* 2013c; Kamilar and Ledogar 2011). Studies of community assembly therefore need to employ spatially explicit methods of analysis that account for the varying contributions of spatial scale (Borcard *et al.* 2004).

Previous tests of primate community assembly have shown that patterns vary across regions in the relative contribution of environmental and spatial effects, operating at local and regional scales. In the neotropics, Africa, and Borneo, dispersal limitation by distance (a spatial effect) better explains primate community assembly than environmental variables (Beaudrot and Marshall 2011; Gavilanez and Stevens 2013; Kamilar 2009), whereas in Madagascar environmental variables better explain patterns in primate composition than spatial effects (Beaudrot and Marshall 2011). Differences in patterns of community assembly may exist owing to intrinsic differences between geographic areas (i.e. climate, biogeography, and evolutionary history) and/or the compounding effects of spatial and temporal scale. However, previous community assembly work in Madagascar (Beaudrot and Marshall 2011; Muldoon and Goodman 2010) has not tested the role of biogeographic barriers in shaping community composition, although Madagascar's mammal communities evolved *in situ* within a biogeographic framework (*sensu* Vences *et al.* 2009). Madagascar is characterized by regionally pronounced and locally steep environmental gradients, patterns of microendemism across taxa, and numerous evolutionary radiations, making it an ideal location within which to examine the roles of deterministic, stochastic, and biogeographic processes (Vences *et al.* 2009).

Previous research on primate community assembly focused on primates alone rather than the broader community (Beaudrot and Marshall 2011; Ganzhorn 1999; Gavilanez and Stevens 2013; Kamilar and Muldoon 2010; Beaudrot *et al.* 2013a, b, c; Muldoon and Goodman 2010), even though primates interact with species from other clades (Emmons *et al.* 1983; Ganzhorn 1999; Gautier-Hion *et al.* 1980). A more inclusive study of all nonvolant mammal communities would not only encapsulate more ecological interactions and functional adaptations to environments, but it would also provide a more comprehensive understanding of species co-occurrence and biodiversity patterns. Previous research on birds, fish, plants, and invertebrates suggested that body size, dispersal limitation, environmental associations, and biogeographic barriers all influence community assembly (Cottenie 2005; Soininen *et al.* 2007). These different assembly processes often interact to result in nonrandom patterns of taxonomic and functional organization.

In this study I use a variation partitioning approach to evaluate the influence of environmental effects, spatial effects, and the dispersal costs of biogeographic barriers in shaping patterns of nonvolant mammal community composition in 34 protected areas across Madagascar. Environmental effects, through species–environment sorting, promote species coexistence (Chase and Leibold 2003; Tilman and Pacala 1993). Assuming species are primarily stenoecious (restricted to specific habitats), variation in vegetation (i.e., environmental heterogeneity) is often an important component in community assembly and largely driven by climatic conditions (e.g. Ackerly 2003).

Consequently, I use climatic variables, including precipitation and temperature to represent environmental effects. Spatial effects (including dispersal limitation) result in spatially structured patterns independent of environmental heterogeneity (Fortin and Dale 2005, Lindo and Winchester 2009). Dispersal limitation occurs when a species cannot colonize another area because the new site is too far away (Chase 2003; Condit *et al.* 2002; Potts *et al.* 2002; Tuomisto *et al.* 2003). Here, I model spatial effects with principal coordinates of neighbor matrices, a scale-explicit method for investigating spatial relationships between communities (Borcard *et al.* 2004). For biogeographic effects I use a ratio of the effective dispersal distance around biogeographic barriers (permanent water bodies, rivers, and the island edge) to the straight-line distance between sites, thereby accounting for the unique contribution biogeographic barriers pose on dispersal.

In addition, I divide the nonvolant mammal communities into different evolutionary lineages, i.e., primate and nonprimate (afrosoricidans, carnivorans, and rodents) and different functional groups (arboreal and terrestrial species). Arboreal species require varying degrees of intact forest, and this forest dependence may compound the roles of dispersal limitation by distance and by biogeographic barriers if the matrix between sites is impassable (Pozo-Montuy *et al.* 2011; Santos-Filho *et al.* 2012). Groups that are arboreally constrained (most primate species), and therefore limited by long-distance dispersal opportunities, will have community structures that are dependent on the distance between sites (Lindo and Winchester 2009). Madagascar is shaped by severe forest fragmentation (DeFries *et al.* 2005; Harper *et al.* 2007), and the matrix between forested sites may be difficult for arboreal species to pass through (Prugh *et al.* 2008). Consequently, I predict spatial effects and biogeographic barriers shape primate communities and arboreal communities more than environmental effects. By contrast, groups that are capable of dispersing long distances (nonprimates and terrestrial species) are not limited by distance but are instead limited by habitat availability and environmental conditions (Lindo and Winchester 2009). Consequently, I predict environmental effects best explain nonprimate mammal communities and terrestrial communities.

Methods

Community Composition

I collected data for 34 protected areas in Madagascar (Fig. 1). I compiled occurrence data for species (orders Afrosoricida, Carnivora, Primates, Rodentia) from published sources of confirmed sighting data to assess the composition of nonvolant mammal assemblages in Madagascar. I used Mittermeier *et al.*'s (2008) taxonomy for primates and Wilson and Reeder's (2005) taxonomy for nonprimates (Table SI) at the species level. I excluded domesticated and nonindigenous species from assemblage lists. I defined an ecological community as all the nonvolant mammal species that potentially interact within a single patch or local area of habitat (Chase and Leibold 2003; Fauth *et al.* 1996), in this case protected areas in Madagascar (ranging from 104 km² to 5899 km²). I identified each species as habitually terrestrial or arboreal based upon descriptions in the primary literature (Table I; Table SI).

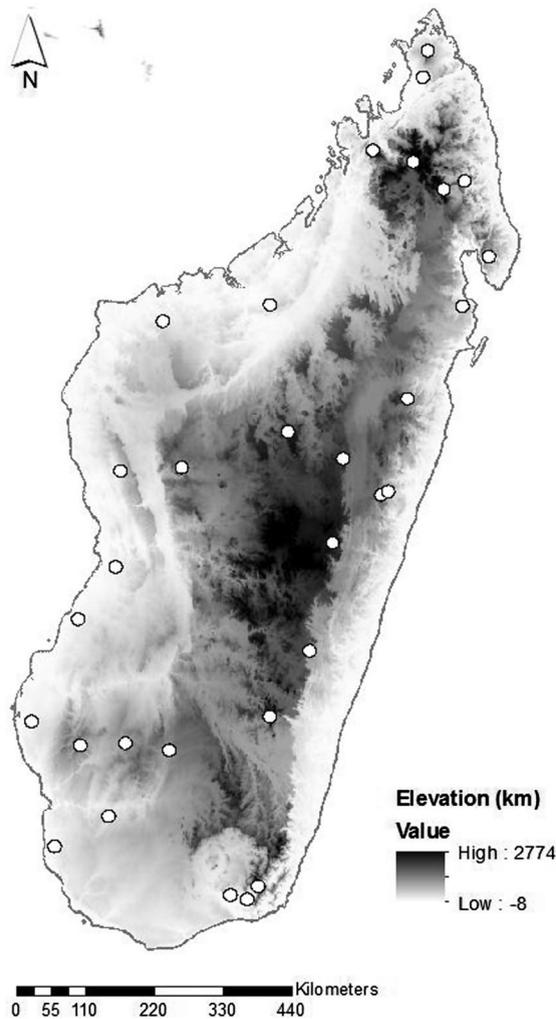


Fig. 1 Locations of study sites in Madagascar included in this study.

Those species that are habitually both arboreal and terrestrial (spend almost equal amounts of time on either substrate type) were included in both terrestrial and arboreal analyses (Table 1).

Quantifying Macroecological Effects Related to Community Assembly

Environmental Effects I used georeferenced data on environmental variables for each study site collected from the Madagascar Digital Elevation Model (CGIAR-SRTM data aggregated to 30 s) (Hijmans *et al.* 2004) and the WorldClim Global Climate Database (Hijmans *et al.* 2005). These bioclimatic variables included elevation, mean annual temperature, mean diurnal range in temperature, isothermality, temperature seasonality, maximum temperature (of warmest month, of coldest month), temperature annual range, mean temperature

Table I Species richness for each nonvolant mammal order in Madagascar reported in this study, including assignments to terrestrial and/or arboreal groups and adult body mass statistics

Order	Terrestrial	Arboreal	Arboreal and terrestrial
Primates	0	69	1
Primate adult body mass (g) ^a			
Mean±SD		1713.50±1967.16	2640
Range		48.50–8650	
Afrosoricida	25	0	4
Carnivora	5	0	3
Rodentia	13	9	2
Nonprimate adult body mass (g) ^a Adult body mass (g) ^a			
Mean±SD	332.20±637.47	970.20±2582.08	1843.34±3436.10
Range	3.4–2800	8.08–9500	8.08–9500

^a Adult body mass data obtained from PanTHERIA (Jones *et al.* 2009) for 70 of the 131 species present in this study

(of wettest quarter, of driest quarter, of warmest quarter, of coldest quarter), precipitation (annual, of wettest month, of driest month, of wettest quarter, of driest quarter, of warmest quarter, or coldest quarter), and precipitation seasonality. I calculated mean values for each environmental variable across a 10 km radius around each study site centroid to ensure that mean values were representative of the protected area, while still being enclosed by the protected area boundaries. Environmental variables were tested for significant autocorrelations (*sensu* Beaudrot and Marshall 2011) using Pearson’s product–moment correlation coefficient. To minimize over-fitting models due to highly correlated environmental variables, I included variables in the analysis if they had a correlation of <0.8 and documented influences on mammal populations (Table II).

Spatial Effects I used principal coordinates of neighbor matrices (PCNM) for the analysis of spatial effects across various spatial scales in the community composition data (Dray *et al.* 2006). The PCNM approach works well with

Table II Variables tested for significant relationships with community composition in this study

Location	Environmental effects ^a	Biogeographic effects	Spatial effects
•Longitude	•Elevation	•Elevation effective distance ratio	•Broad scale (PCNMs 1–5)
•Latitude	•Mean annual temperature	•Permanent water bodies and rivers	•Medium scale (PCNMs 6–10)
	•Temperature seasonality	•Effective distance ratio	
	•Annual precipitation	•Island edge effective distance ratio	
	•Precipitation seasonality		

All variables were included in each global model for each community grouping (primates, nonprimate mammals, arboreal mammals, terrestrial mammals) and each effect type (location, environmental, biogeographic, spatial), followed by a forward selection procedure to select variables for reduced models

^a Variables shown here are those with Pearson’s product–moment correlation coefficient of <0.8

presence/absence data and community data from multiple sites across space (Legendre *et al.* 2005). Further, it can be used to detect significant correlations of community composition with environmental variables independent of spatial autocorrelation at a variety of spatial scales (Borcard and Legendre 2002; Borcard *et al.* 2004), which is important with geographically distributed data (Fortin and Dale 2005; González-Megías *et al.* 2005).

PCNM analysis creates spatial predictors that can be directly included in regression models by computing eigenfunctions of spatial connectivity matrices (Griffith and Peres-Neto 2006). PCNM uses a principal coordinate analysis of a Euclidean distance matrix among study sites. The analysis truncates each matrix at the smallest distance between nearest neighbors that keeps all sites connected in a single network (*ca.* 26 km). The eigenvectors (PCNMs) that modeled positive spatial correlation (Moran's I larger than expected value of Moran's I) were retained and used to represent spatial structuring in patterns of community composition. The first PCNMs represent broad scale spatial structures, with successive PCNMs representing progressively smaller spatial scale effects (Borcard and Legendre 2002), ranging between 1400 km (broadest scale) and 26 km (smallest scale). Consequently, PCNMs with positive eigenvectors were evenly separated into small, medium, and broad spatial scales to reflect the spatial grain of the study sites (*sensu* García *et al.* 2011). The use of the terms "small," "broad," and "medium" scales were defined relative to this particular set of study sites and were constrained by the data's resolution and spatial extent. PCNM variables were created using the R package PCNM (Legendre *et al.* 2010), based on geographic coordinates for each study site centroid. I calculated the geographic coordinates from the protected area boundaries (Gerber 2010) in ArcGIS 10.1 (Feature to Point tool) for each site.

Biogeographic Effects I measured biogeographic effects as an effective distance ratio for each type of biogeographic barrier considered (permanent rivers and bodies of water, elevation slope, and the island edge). Data on biogeographic dispersal barriers were extracted from digital maps of Madagascar (e.g. Fig. 1), including permanent rivers and bodies of water (Lehner and Doll 2004), elevation slope (Hijmans *et al.* 2004), and the island edge (Hijmans *et al.* 2004). Elevation slope was divided into four equal categories of 22.5° increments (maximum of 90°). Least-cost paths (LCPs) were calculated as measures of the effective distance between each unique site pair based on the costs of crossing over or around biogeographic barriers. Using the Spatial Analyst extension in ArcGIS version 10.1 (ESRI) and a custom Python script, I performed the LCP analysis in which the path resulting in the lowest cost to reach a target site from the origin site was identified. LCPs between sites were measured with a friction layer that depicted the cost of crossing a habitat with biogeographic barriers present. A simple model was used where a prohibitively high cost (cells were set to "NoData" to make them impassable) was assigned to biogeographic barriers (permanent water bodies, permanent rivers, and the island edge) and remaining habitat had no cost assigned to it. The 0–45° slope increments were assigned the lowest travel cost (value of 9, on a scale from 1 to 9 with 9 being the lowest), the 45°–70.5° increment was assigned a

moderate cost (value of 5), and 70.5°–90° the highest and most prohibitive cost (value of 1). These divisions and assigned costs were chosen to reflect the energetic costs of traveling over terrains with higher travel costs (sensu Wade *et al.* 1998). Effective distance ratios were then calculated for each site. For n sites numbered 1 to n , the effective distance ratio of site i , denoted DR_i , was defined as

$$DR_i = \sum_{1 \leq j \leq n, j \neq i} \frac{d^*(i, j)/d(i, j)}{n-1},$$

where $d^*(i, j)$ was the effective distance between sites i and j and $d(i, j)$ was the Euclidean distance between sites i and j . This measure reflects the effective distance between sites and degree of site isolation. I conducted this analysis separately for every unique site pair and each type of barrier. Where biogeographic barriers did not exist, the Euclidean distance was equal to the effective distance (ratio of 1). Where biogeographic barriers imposed travel costs the effective distance was longer than the Euclidean distance and the effective distance ratio was >1 .

Modeling Macroecological Effects on Community Composition

All analyses were conducted in R 2.15.3. I modeled the multivariate response of Madagascar's 1) nonvolant mammal communities, 2) primate communities, 3) nonprimate nonvolant mammal communities, 4) arboreal nonvolant mammal communities, and 5) terrestrial nonvolant mammal communities to a matrix of environmental variables, spatial variables (PCNMs), and biogeographic effective distance ratios using variation partitioning techniques. In this modeling approach community composition was the response variable, and the environmental, spatial, and biogeographic variable sets were the explanatory variables. Before analysis, community composition matrices (species \times site) were Hellinger transformed to allow using redundancy analysis (RDA) without considering the common absence of a species as a resemblance between communities (Legendre and Gallagher 2001).

Community composition data were checked for the presence of linear trends (trend between composition and geographic coordinates) using RDA and an ANOVA with 1000 permutations. A significant trend indicated the presence of spatial effects at broader scales than the sampling extent, or a gradient across the entire studied area (Borcard *et al.* 2004). Composition should be detrended for PCNM analysis, or a large number of PCNMs would be necessary to model the linear trend in composition and their role in modeling finer spatial scales might go unnoticed (Borcard *et al.* 2004). Where the linear trend was significant composition was detrended; composition matrices were regressed against longitude and latitude and the residuals retained as response variables (sensu Borcard *et al.* 2004; Legendre and Legendre 2012). Both nondetrended and detrended (where applicable) composition matrices were retained for analysis because including the linear trend in composition (nondetrended) was equivalent to modeling the spatial pattern of composition at the broadest spatial scale (all of Madagascar), while detrending allowed for modeling smaller spatial scales (detrended).

Global models (with complete sets of explanatory variables, Table II) for each community grouping and effect type (location, environmental, biogeographic, spatial) were tested for significance with a RDA and an ANOVA with 1000 permutations, from which the global adjusted R^2 value was calculated. I then used a forward selection procedure to retain the variables (latitude and longitude, PCNMs, environment, biogeographic) with the highest explanatory power while preserving interactions between variables and producing the most parsimonious model (Legendre and Legendre 2012). For each significant global model, a forward selection with 9999 Monte Carlo permutation tests was done, and a double stopping criterion was used where the selection stopped if either a P -value of 0.05 or the global adjusted R^2 were exceeded (Blanchet *et al.* 2008). I repeated the forward selection process for each variable group and each taxonomic/functional group individually. The RDA and tests of significance were computed with the `rda` and `anova.cca` functions of the `vegan` library in R (Oksanen *et al.* 2008), and the `forward.sel` function in the `packfor` package (Dray *et al.* 2011) was used for forward selection.

Variation partitioning was then used to identify the components of variation in community composition explained by environmental effects, biogeographic barriers, and spatial effects (Gilbert and Lechowicz 2004; Jones *et al.* 2008; Kamilar 2009; Legendre *et al.* 2005; Lindo and Winchester 2009). Variation partitioning was carried out using the `varpart` function of the `vegan` R package (Oksanen *et al.* 2008), which uses RDA to compute the variation attributable to each set of explanatory variables. I used the adjusted R^2 statistic to assess the proportion of the response variation explained by each explanatory data set and their combinations. The adjusted R^2 provides unbiased estimates of the explained variation (Peres-Neto *et al.* 2006). Only variables selected in the forward selection procedure were included in the variation partitioning analyses. I used partial RDAs and ANOVAs to test the significance of each pure component of variation while controlling for other variable sets. For example, I tested the amount of variation due to environmental effects for significance while controlling for spatial and biogeographic effects. Where variation was shared between PCNMs and other components of variation (environmental variables and biogeographic effective distance ratios), that component of shared variation was interpreted as spatially structured (*sensu* Laliberté *et al.* 2009). Dividing the PCNMs into broad, medium, and small spatial scales showed the amount of variation attributed to those spatial scales.

Variation partitioning was run in two ways across the five community groups: *model 1*: using forward selected environmental variables, PCNMs (small, medium, broad scale), biogeographic effective distance ratios, and the linear trend of geographic location (longitude and/or latitude) without detrending composition; and *model 2*: using forward selected environmental variables, PCNMs (small, medium, broad scale), biogeographic effective distance ratios, and detrended composition (*sensu* Borcard *et al.* 2011). Several components of variation are reported: pure effects where the variation was attributable to a single source, e.g., pure environmental effects; total effects where the total amount of variation is attributable to a source and its covariations with other variables, e.g., total environmental effects; and shared spatial-environmental effects (the shared variation of environmental and spatial effects). I considered statistical tests significant at $P < 0.05$.

Results

Patterns of Community Composition

Of 131 nonvolant mammal species in this study, 70 were primates, representing 5 families and 15 genera (Table SI). The remaining 61 nonprimate mammals represented 3 orders (Afrosoricida, Carnivora and Rodentia), 3 families, and 24 genera (Table SI). Alpha diversity (the number of species present at each study site) ranged from 11 to 42 species, including 3–13 primates and 5–30 nonprimate species at each site. I classified 78 species as arboreal, 43 terrestrial, and 10 as habitually both terrestrial and arboreal (Table SI).

Significant linear trends between composition and location (latitude and longitude) were present in all five community types: all nonvolant mammals ($F = 6.57$, $df = 2$, $P < 0.001$), primates ($F = 6.44$, $df = 2$, $P < 0.001$), nonprimates ($F = 6.45$, $df = 2$, $P < 0.001$), arboreal mammals ($F = 6.19$, $df = 2$, $P < 0.001$), and terrestrial mammals ($F = 6.71$, $df = 2$, $P < 0.001$). Twenty-two PCNMs were present in the data sets with 10 eigenvectors with positive spatial correlations. These 10 eigenvectors represented 2 spatial scales: broad (PCNMs 1–5) and medium (PCNMs 6–10) (Fig. S1). No small-scale spatial structures were positive and/or significant (PCNMs 10–20). PCNM 1 describes a latitudinal gradient in nonvolant mammal community composition, where the north and south of Madagascar are differentiated, and PCNM 2 describes a combination of a latitudinal and longitudinal division between mammal communities in the northeast and those in the southwest (Fig. S1). All five composition matrices were detrended owing to significant linear trends and used for model 2 analyses. Owing to similarities in overall results between model 1 and model 2, model 2 results are in the Electronic Supplementary Material.

Biogeographic Effective Distances

Results suggest that biogeographic barriers created additional dispersal costs for species moving between study site locations (Table III), and these costs were dependent on the relative locations of biogeographic barriers. Mean effective distances were highest when subjects were traveling over elevation changes (608.18 km), and the lowest when traveling around permanent water bodies (596.51 km). The ratio of effective distance to Euclidean distance followed a similar pattern. However, the sites that had the highest mean effective distances and the highest ratio differed (Table III).

PCNM Analyses and Forward Selection

Model 1 (Nondetrended Data) The global PCNM analyses were significant for all taxonomic groupings: nonvolant mammals ($F = 2.91$, $df = 10$, $P < 0.001$), primates ($F = 3.53$, $df = 10$, $P < 0.001$), nonprimate mammals ($F = 2.47$, $df = 10$, $P < 0.001$), arboreal mammals ($F = 3.18$, $df = 10$, $P < 0.001$), and terrestrial mammals ($F = 2.66$, $df = 10$, $P < 0.001$). For all community groupings, latitude and longitude were significant in the forward selection procedure (Tables SII and SIII), meaning that significant linear trends in community composition along both latitude and longitude in Madagascar were present. Significant environmental variables were the same for nonvolant mammals,

Table III Comparison of straight line (Euclidean) and biogeographic effective distances (including biogeographic barriers) between 34 study sites in Madagascar

	Euclidean distance (km)	Island edge	Permanent water bodies	Elevation changes
		Biogeographic effective distances (km)		
Mean ± SD	562.76±94.95	598.48±102.05	596.51±101.28	608.18±104.82
Range	434.16–794.96	461.79–843.90	460.84–847.66	467.35–862.17
		Biogeographic effective distance ratios		
Mean ± SD		1.06±0.015	1.06±0.015	1.08±0.020
Range		1.05–1.12	1.03–1.11	1.06–1.13

Site averages, calculated from a site-by-site distance matrix, are presented. The biogeographic effective distance ratio is the ratio of each biogeographic effective distance to the Euclidean distance. It is a measure of how isolated a site is, and considers the unique role different biogeographic barriers have on the effective dispersal distance between sites

primates, and arboreal mammals, although in different orders, and included annual temperature, annual precipitation, temperature seasonality, and precipitation seasonality (Tables SII and SIII). Annual temperature, annual precipitation, temperature seasonality, and elevation significantly described nonprimate mammals and terrestrial mammals (Tables SII and SIII). Nonvolant mammals, primates, and arboreal mammals also had the same seven significant PCNMs (Tables SII and SIII). These seven PCNMs described both broad- and medium-scale structures in community composition (Fig. S1). Terrestrial mammals and primates had the same four significant PCNMs (Tables SII and SIII) depicting broad-scale structuring of compositional patterns. The biogeographic effective distance ratio accounting for the cost of traveling within the island edge was significant for all five taxonomic groupings.

Variation Partitioning

Model 1 (Nondetrended Data) Environmental and spatial (PCNMs) variables significantly shaped nonvolant mammal communities, whereas geographic location and biogeographic barriers (effective distance ratio) played less important and nonsignificant roles (Fig. 2; Table SII). I excluded biogeographic barriers from the variation partitioning models explained below due to nonsignificant and very small contributions to nondetrended community composition for all groups. Instead, the variation partitioning models included environmental effects, geographic location, broad-scale PCNMs, and medium-scale PCNMs (Fig. 2; Tables SII and SIII). Of the explained variation, pure spatial (7.3%), pure environmental (7.0%), and shared environmental and broad-scale spatial effects (7.2%; Fig. 2; Table SII) shaped nonvolant mammals almost equally. Of the spatial effects, broad-scale (3.7%) and medium-scale (3.6%) proportions of variation were almost equal (Table SII). Location explained a small portion of nonvolant mammal communities (2.0%). Primate and arboreal mammal communities had more of their explained variation due to spatial effects (11.2%, 9.8%, respectively) than environmental effects (5.7%, 7.5%, respectively), and broad-scale effects (6.0%, 5.1%, respectively) explained amounts of variation similar to those of medium-scale effects (5.2%, 4.7%, respectively; Tables SII and SIII). In addition,

covarying effects, with 8–10% of compositional variation explained by joint broad-scale spatial and environmental effects, explained most of the variation by environmental and spatial effects in primate and arboreal mammals (Tables SII and SIII). Only 2.3% and 2.0% of the variation in primate and arboreal mammal communities respectively was due to location. For nonprimate and terrestrial mammals spatial effects explained a very small and nonsignificant proportion of variation (1.3%, 1.8%, respectively), with environmental effects (12.4%, 10.8%, respectively) explaining six and five times more of the variation, respectively (Tables SII and SIII). The combined environmental and spatial variation in nonprimate (2.5%) and terrestrial mammal communities (3.7%) was a small part of the total variation explained by the model (Tables SII and SIII). Nonprimate and terrestrial mammals had 2.5% and 1.8% (not significant) of their variation respectively due to location, which was greater than the contribution of spatial broad-scale effects for both groupings. Across groups primate and arboreal mammal models explained the largest proportion of nondetrended community composition (range = 48.9–50.1% explained variation; Fig. 2; Tables SII and SIII).

Discussion

Environmental and spatial effects almost equally shaped nonvolant mammal communities in Madagascar. Contrary to predictions, biogeographic barriers, measured as effective dispersal distance ratios, did not significantly shape any community. As predicted, however, variation in primate and arboreal mammal communities was mostly due to spatial effects. In addition, environmental effects explained all of the compositional variation for nonprimate and terrestrial mammals. These results provide support for functional differences between taxonomic groups as important considerations in the study of community assembly.

Previous community assembly research in Madagascar found that Madagascar's primate (Beaudrot and Marshall 2011; Kamilar 2009) and nonvolant mammal

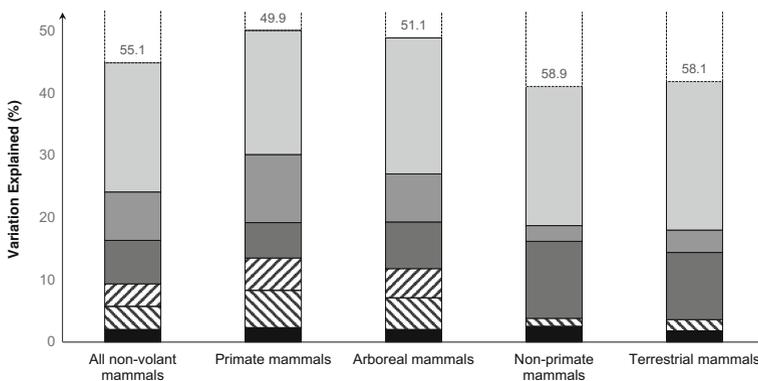


Fig. 2 Percent of variation in community composition explained by location, environmental, biogeographic, and spatial effects for 34 nonvolant, primate, arboreal, nonprimate, and terrestrial mammal communities in Madagascar. For clarity, unexplained variation is a numeric value at the top of each column. This figure includes only model 1 (undetrended composition) results; see Figure S1 and Tables SII and SIII for additional results.

communities (Muldoon and Goodman 2010) sort with environmental variables. However, a significant distance effect in the mammal communities across the island also existed (Muldoon and Goodman 2010). Regardless of geographic location, i.e., longitude and latitude, this study shows that nonvolant mammal community composition is shaped by spatial effects occurring at broad and medium spatial scales, and the contribution of these spatial effects is equal to the contribution of environmental effects.

Madagascar has substantial environmental gradients with high climate variability (Dewar and Richard 2007). In this study, environmental effects were weakly related to medium spatial scales and strongly related to broad scales. The climatic variables that were forward selected (*not detrended*: precipitation and temperature, *detrended*: elevation) are broad-scale features that characterize ecoregional differences in Madagascar (Dewar and Richard 2007; Donque 1972; Muldoon and Goodman 2010). Eastern Madagascar has the most rain because of orographic precipitation, whereas the west is hotter and drier (Jury 2003). Differences in community composition in nonvolant mammal communities are therefore characterized not only by geographic distance (Muldoon and Goodman 2010; and this study) but also by differences in broad-scale environmental variables, such as precipitation (Kamilar and Muldoon 2010; Muldoon and Goodman 2010; and this study). Further, patterns of temperature and precipitation seasonality were significant factors shaping all nonvolant mammals (*sensu* Dewar and Richard 2007) when not detrended. The observation that precipitation and rainfall were not significant variables when community composition was detrended (effect of location removed) and spatial effects were better explanations for patterns in community composition further supports the importance of ecoregional differences driving community assembly in Madagascar.

Primates and Arboreal Mammals vs. Nonprimates and Terrestrial Mammals

Overall, primate communities and arboreal communities were very similar because primates made up >88% of arboreal community diversity. Spatial effects strongly shaped both primate and arboreal mammal communities but biogeographic effects were not significant. Because all primate species in Madagascar are at least somewhat arboreal, spatial effects similarly shaped primates and arboreal mammals. Interestingly, spatial effects explained more of the variation in composition for primates than for arboreal mammals. Primates in Madagascar have on average larger body sizes ($\bar{x} = 1713 \text{ g} \pm 1967 \text{ g}$) and are potentially more restricted in their habitat requirements than the smaller bodied arboreal nonprimate mammals ($\bar{x} = 970 \text{ g} \pm 2582 \text{ g}$; Table I). Larger bodied arboreal animals require larger substrates for travel and support (*sensu* Remis 1995; Warren and Crompton 1997), additionally constraining their distribution and affecting the assembly processes most likely to affect their community composition. However, recent work has shown that body mass is phylogenetically conserved in Malagasy primates and not shaped by environmental variables or space (Kamilar *et al.* 2012). Body size might not be driving the importance of spatial effects in primate and arboreal mammal communities. Instead, habitat dependence on resources, including food availability, may drive this pattern. Madagascar's primates have flexible ecological requirements (Kamilar 2009; Kamilar and Muldoon 2010; Kamilar *et al.* 2012), with unique

suites of adaptations, e.g., low basal metabolic rates, unusual life-history patterns, small group sizes, to high climatic variability (Dewar and Richard 2007). In this study both temperature and precipitation seasonality, when not detrended, significantly shaped primate and arboreal mammal communities. It is possible that primate ecological flexibility dampens the importance of environmental effects in comparison to the contribution of spatial effects on primate and arboreal mammal communities.

In contrast to primate and arboreal mammal communities, only environmental effects explained nonprimate mammal and terrestrial mammal communities. Nonprimate mammal and terrestrial mammal communities had very similar species composition, because nonprimate species made up 98% of the diversity in terrestrial communities. Elevation was a significant environmental variable for nonprimate and terrestrial mammals in both models (nondetrended and detrended) whereas it was significant only for detrended composition in primate communities. Elevation is a previously documented important environmental variable for mammals in Madagascar (Goodman and Rasolonandrasana 2001; Goodman *et al.* 1996, 1999). In addition, climatic trends in small mammal diversity exist, with peaks occurring with mountain height (McCain 2005). Small mammals are potentially responding to a climatic optimum, which may exist below the persistent cloud cover at the top of mountains (Goodman *et al.* 1999; McCain 2005). The absence of elevation slope changes (a biogeographic variable) and the presence of elevation, precipitation, and temperature as significant environmental variables shaping nonprimate and terrestrial mammal communities suggest that the climatic features associated with elevation are helping shape community composition. The contribution of elevation to patterns of community composition may also result from historical patterns of allopatric speciation, due to population isolation in river watersheds of different elevational ranges during Quaternary climate change (Wilmé *et al.* 2006). Evidence of such allopatric speciation exists for diurnal primates (Wilmé *et al.* 2006), but has had mixed support in other fauna, e.g., *Eliurus myoxinus* (Shi *et al.* 2013) and reptiles (Pearson and Raxworthy 2009).

The finding that spatial effects were more important to primates and arboreal mammals than to terrestrial and nonprimate mammals is not surprising because habitat requirements restrict arboreal animals (of which most were primates). Grassland edged with diverse woodlands covers (at least) 72% of Madagascar (de Wit 2003). Consequently, the distance between sites and the nature of the matrix between protected areas probably place different demands on dispersing species. In Madagascar, a country shaped by marked habitat change over the last 2000 years and severe forest fragmentation (DeFries *et al.* 2005; Harper *et al.* 2007), arboreal species are predicted to be highly dispersal limited because the matrix between forested sites may be difficult to pass through (Prugh *et al.* 2008). Further, the central highlands of Madagascar present a significant barrier to faunal dispersal (Muldoon and Goodman 2010). A matrix of anthropogenic habitat between sites is probably unsuitable for most Malagasy primate species (Schwitzer *et al.* 2011), although some species, such as *Microcebus* and *Mirza*, thrive in anthropogenic habitats (Ganzhorn 1987; Ganzhorn 1999; Irwin *et al.* 2010). Further, primate (and reptile) dispersal in Madagascar is highly geographically constrained, and most species are endemic to only 25% of Madagascar's surface area (Pearson and Raxworthy 2009).

Biogeographic Barriers

My measure of site isolation (biogeographic effects) did not explain patterns in community composition regardless of taxonomic grouping. In addition to the potential error in assigning cost values to barriers used to generate dispersal surfaces, this unexpected finding has three possible explanations. First, the effect of rivers and water bodies as biogeographic barriers may be too species specific to see at a community level, and biogeographic effective distance had an averaging effect by looking at entire communities. Rivers are biogeographic dispersal barriers for a variety of Malagasy species when investigating species range limits (Goodman and Ganzhorn 2004b). However, my community level of analysis may have subsumed species level variation in biogeographic barriers. For example, several *Eulemur* species are not affected by rivers and have ubiquitous distributions, while other lemur genera including *Indri* and *Propithecus* (some species) are biogeographically constrained by the position and size of some rivers (Goodman and Ganzhorn 2004b). Further, detailed survey data in a variety of habitat types is lacking for many species (cf. Goodman and Ganzhorn 2004b), limiting documented environmental and biogeographic limits of many species. A useful avenue for future research would be to evaluate both the taxonomic and functional, e.g., body size or locomotion, specificity of dispersal costs around biogeographic barriers.

Second, by considering all permanent water bodies, as opposed to those that have already been supported as important biogeographic barriers, e.g., Bemarivo River, Lokoho River, Antainambalana River, Mangoro River, Mananara River (Goodman and Ganzhorn 2004b), my analysis may have concealed the effect of the few and significant biogeographic barriers that exist. These previously established important biogeographic barriers may be unique in their size, elevational distribution, and position of their sources or headwaters (sensu Goodman and Ganzhorn 2004b; Wilmé *et al.* 2006). Although these rivers potentially constrained the distribution of species thousands of years ago, today they might not be the strongest contributors to mammal distributions in Madagascar.

Third, the ecological history of Madagascar is under debate. The assumption that primary forest covered Madagascar prior to human arrival is contested (Burney *et al.* 2003; Klein 2002; Muldoon *et al.* 2012). Either Madagascar was a forest–woodland–grassland mosaic (Burney 1997; Muldoon *et al.* 2012) that shifted to grasslands by the action of fires (Burney 1996), or a forested corridor existed westward across the southern part of the highlands, allowing for faunal dispersal (Muldoon *et al.* 2012). The compositional differences in mammal communities between east and west Madagascar is suggested as evidence of past faunal exchange across the Central Highlands (Muldoon and Goodman 2010), resulting in damped differences between community composition. Moreover, terrestrial fauna may have dispersed more easily than arboreal fauna, accounting for the lack of spatial effects detected in the community composition for nonprimates and terrestrial mammals. The biogeographic complexity and varying patterns of faunal endemism in Madagascar make recovering highly congruent patterns of vicariance events unlikely (Pearson and Raxworthy 2009), and may limit the ability of a single index to reveal salient patterns in community composition.

Although previous research considered the distance between sites or the spatial characteristics of a biogeographic area as indicators of historical, regional, or

biogeographic processes acting (Beaudrot and Marshall 2011; Kamilar 2009), the relationship between distance and historical and biogeographic process is unclear. PCNMs are suggested good proxy measures for historical events in Neotropical primates that may also represent the role of dispersal limitation by distance (Gavilanez and Stevens 2013). Further, a measure of dispersal limitation (as geographic distance) can be the result of both stochastic dispersal limitation and historical/biogeographic processes because of variation in dispersal ability or speciation among taxa resulting in a geographic distance effect in taxonomic patterns of primate communities (Kamilar 2009). However, investigating spatial effects and biogeographic barriers as separate entities can help identify the variation in community structure that is separately due to dispersal limitation, additional spatial effects, and biogeographic barriers. Using a scale explicit approach for investigating assembly can help reveal the relative importance of each process against a complex background of processes operating at various spatial scales (Chase and Myers 2011). Although neither the biogeographic effective distance ratios nor the shared spatial–biogeographic variation explained patterns of composition in this study, the study of different barriers (refugia and watersheds; *sensu* Vences *et al.* 2009), barrier metrics, different groups, or different biogeographic regions may consequently reveal greater contributions of biogeographic processes to community assembly.

Methodological Challenges

The absence of small spatial scale structures in these data is potentially due to the scale at which I was able to describe the communities. Because they were the total species composition of an entire protected area, the sampling may be at too large a grain to account for fine-scale spatial patterns. The absence of these fine-scale structures highlights the need for more detailed surveys within more protected areas to account for local-scale processes that may be shaping composition, including inter- and intra-specific competition (Kamilar and Ledogar 2011).

The amount of explained variation in community composition in this study was between 6 and 50%, leaving large amounts of community variation unexplained. Separating the covarying effects of community assembly processes requires further elucidation of the biogeographic and environmental variables that influence them. In addition, pure spatial effects may hide unmeasured spatially structured environmental or deterministic variables (Borcard and Legendre 1994; Jones *et al.* 2008). A further possibility is that the variables I initially selected may not be ideal for detecting community assembly processes in mammal communities. Although unexplained variation can highlight hidden variables, a high unexplained fraction of variation is likely common in ecological data (ter Braak and Prentice 1988). Further, many other studies have also found large unexplained fractions (range = 20–49%; Cottenie 2005; Gavilanez and Stevens 2013; Gilbert and Lechowicz 2004; Jones *et al.* 2008).

Conclusions

Community assembly is complex, and processes are not mutually exclusive. Instead of being generalizable by taxa, functional traits, e.g. arboreal vs. terrestrial, may better

describe patterns in community assembly. In this study, variables used to indicate the operation of deterministic, stochastic, and biogeographic processes differentially shaped terrestrial mammal communities from arboreal mammal communities. Spatial effects best explained arboreal mammal communities (and primates), whereas terrestrial mammal communities (and nonprimate mammals) were best explained by environmental effects. Future studies and comparisons of Madagascar's primate communities may benefit from trait-specific analyses of ecological processes because niche differences, which stem from trait-level differences, shape deterministic processes. The role of spatial effects were shown here to be more important to arboreal fauna than to terrestrial fauna, a logical result if the extant matrix between sites in Madagascar is impassible, and is also a potential by-product of severe habitat disturbance. This difference in the relative contribution of community assembly processes to different taxonomic groupings highlights an alarming conservation concern for the arboreal mammals and primates of Madagascar, as continued habitat modification is likely to impact their dispersal. Research is needed to identify the unique contribution anthropogenic disturbance has on patterns of community assembly because predictive models for future community-level changes with continued land modification are required for evidence-based conservation and management practices.

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Supporting Information Model 2 results, Tables SI–SIII, and Fig. S1 are available online.

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Erratum to: Primate and Nonprimate Mammal Community Assembly: The Influence of Biogeographic Barriers and Spatial Scale

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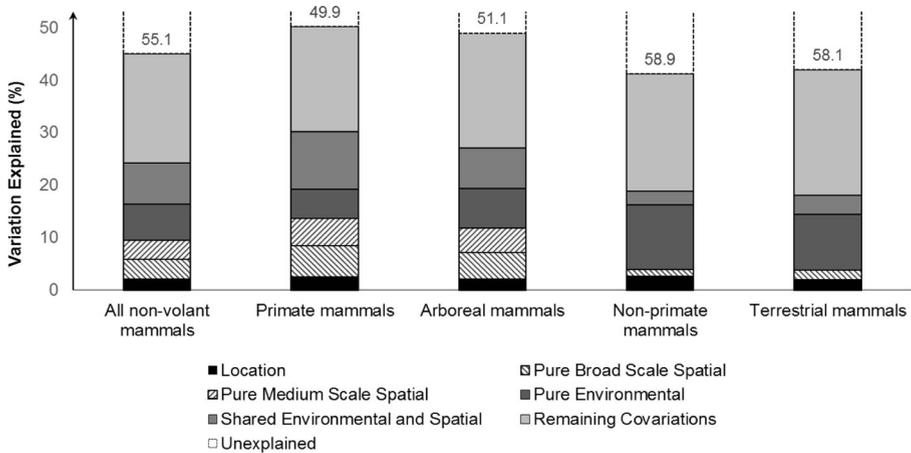
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The original version of this article unfortunately contained a mistake. The updated Fig. 2 bearing the legends was not used during processing.

The missing figure legends are included below:



The author is not liable for the mistake.

The online version of the original article can be found at <http://dx.doi.org/10.1007/s10764-014-9792-2>.

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