Primate communities are structured more by dispersal limitation than by niches

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Summary

1. A major goal in community ecology is to identify mechanisms that govern the assembly and maintenance of ecological communities. Current models of metacommunity dynamics differ chiefly in the relative emphasis placed on dispersal limitation and niche differentiation as causal mechanisms structuring ecological communities. Herein we investigate the relative roles of these two mechanisms in structuring primate communities in Africa, South America, Madagascar and Borneo.

2. We hypothesized that if dispersal limitation is important in structuring communities, then community similarity should depend on geographical proximity even after controlling for ecological similarity. Conversely, if communities are assembled primarily through niche processes, then community similarity should be determined by ecological similarity regardless of geographical proximity.

3. We performed Mantel and partial Mantel tests to investigate correlations among primate community similarity, ecological distance and geographical distance. Results showed significant and strongly negative relationships between diurnal primate community similarity and both ecological similarity and geographical distance in Madagascar, but significant and stronger negative relationships between community similarity and geographical distance in African, South American and Bornean metacommunities.

4. We conclude that dispersal limitation is an important determinant of primate community structure and may play a stronger role in shaping the structure of some terrestrial vertebrate communities than niche differentiation. These patterns are consistent with neutral theory. We recommend tests of functional equivalence to determine the extent to which neutral theory may explain primate community composition.

Key-words: coexistence, community assembly, continental comparison, neutral theory, vertebrate

Introduction

A major goal in community ecology is to identify the mechanisms that govern the assembly and maintenance of ecological communities. Current models of metacommunity dynamics differ chiefly in the relative importance they attribute to two mechanisms hypothesized to structure ecological communities: (i) dispersal limitation and (ii) ecological niche differentiation through interspecific competition and species sorting along ecological gradients (Leibold *et al.* 2004; Holyoak, Leibold & Holt 2005). We investigate the relative roles of dispersal limitation and niche differentiation in structuring resident terrestrial vertebrate communities in four biogeographical regions through analysis of data on primate communities in Africa, South America, Madagascar and Borneo.

An ecological community can be defined as a group of trophically similar species that actually or potentially compete in a local area for the same or similar resources (Hubbell 2001). Community composition refers to the species found at a site and can be measured with either presence-absence or abundance data (Legendre, Borcard & Peres-Neto 2005). Herein we define communities as the primate species present at a particular locality. We acknowledge that the full set of species that compete with primates likely includes non-primate taxa (Estrada & Coates-Estrada 1985; Ganzhorn 1999; Marshall, Cannon & Leighton 2009). Nevertheless, it has generally been argued that primate communities within regions are composed of ecologically similar species and they

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are frequently viewed as self-contained communities (Fleagle & Reed 1996; Fleagle, Janson & Reed 1999). Moreover, primates have been well studied at a large number of sites and their presence or absence can be reliably established through surveys. Consequently, more comprehensive community composition data are available for primates than for any other mammalian taxon, particularly in the tropics. The data available on contemporary primate community composition are simply a snapshot in time of continuously changing communities. As we are unable to track long-term fluctuations in primate community composition, we must rely on the resulting present-day patterns to infer the processes that produced them.

When addressing biogeographical spatial scales and evolutionary time scales, the term metacommunity describes local communities linked by the dispersal of multiple potentially interacting species within the regional species pool (Hubbell 2001). Although several metacommunity models predict that dispersal limitation will affect community structure (Leibold *et al.* 2004), neutral models place particular emphasis on the importance of dispersal limitation as a key mechanism shaping community composition. According to neutral theory (Hubbell 2001), the three parameters expected to govern the community structure are metacommunity size, speciation rate and dispersal rate. The community composition is expected to drift stochastically over time because dispersal and recruitment limitation, in which species fail to reach or establish in all sites favourable to their survival (Hurtt & Pacala 1995), results in competitively inferior species persisting in sites when the competitively superior species for the sites is unable to reach them (Hubbell 2005).

At biogeographical scales, predictions of neutral theory assume the contiguity of metacommunities so that all species have the opportunity to disperse to each site within the metacommunity. For this reason, we investigate primate metacommunities in areas of generally contiguous tropical forest cover. We limit our study to areas of tropical forest cover in order to reduce the potential effects of changes in ecosystems preventing the dispersal of some species (e.g. savanna ecosystems might prevent exclusively arboreal forest-dwelling species from dispersing across open areas). We repeated our analysis using only sites where the most common species in each region was found in order to test our hypotheses where the assumption of metacommunity contiguity is demonstrably valid. The presence of the same taxon at all sites demonstrates that all sites within the metacommunity have been accessible to dispersing individuals and therefore provides a more conservative test.

Most research in primate community ecology has focused on the ecological underpinnings of niche differentiation. Previous research has addressed factors that may differentiate niches within communities, such as body size, activity pattern, diet and canopy use (Cannon & Leighton 1994; Marshall, Cannon & Leighton 2009; Schreier *et al.* 2009). Several regional compilations report the presence or absence of primate species in particular habitat types (Fleagle, Janson & Reed 1999), suggesting that the ecological

factors that determine habitat specialization might influence primate community composition, but the habitat categories used are typically course-grained and discussions of the effects of habitat type on primate community structure have remained largely descriptive. However, cluster analysis of Neotropical primate communities found that communities were clustered by both forest type and geographical region (Peres & Janson 1999), suggesting the importance of both ecological and spatial factors in structuring primate communities. Only a handful of additional studies have quantitatively considered factors affecting primate community composition across communities (Peres 1997; Ganzhorn 1998; Lehman 2006). In this study we are interested in the extent to which variation in community composition between sites is related to ecological and spatial gradients and how the relative importance of these factors varies between regions. We therefore investigate niche differentiation in the form of species sorting along environmental gradients. Species sorting along environmental gradients refers to the idea that if species are most competitive under resource conditions to which they are best adapted, then any given community will be composed of the individual species that are best suited for its particular environmental conditions.

The most comprehensive biogeographical study of primate community structure to date found that both ecological and spatial factors predict community composition (Kamilar 2009). Kamilar (2009) used canonical correspondence analysis (CCA) to evaluate a small set of environmental characteristics, longitude and latitude. The effects of these factors were measured at a continental scale, however, and it is unclear to what extent dispersal between all localities was possible. Our study is better able to test the relative importance of dispersal limitation and niche differentiation by restricting the scale of the analysis to areas of more or less contiguous forest cover rather than entire continents. Our analysis therefore adheres more closely than previous ones to the assumption that species can disperse among all sites within the metacommunity (although this is less true for Madagascar) and is therefore better able to distinguish between dispersal limitation and environmental effects. We also include a more comprehensive set of ecological variables, including net primary productivity, additional climatic variables and soil characteristics (Table 1), thereby increasing the likelihood that we incorporated a biologically realistic characterization of non-human primate habitats.

Herein we present a test of dispersal limitation in residential (i.e. non-migratory) terrestrial vertebrates with data on primate communities from Africa, South America, Madagascar and Borneo (Fig. 1). If dispersal limitation has been important in structuring these metacommunities, then community similarity will depend predominantly on geographical distance: the species composition of communities that are close together will be more similar than that of communities that are more geographically distant, regardless of ecological similarity (Chase *et al.* 2005). Conversely, if communities have been primarily assembled

Table 1. Ecological variables considered. Variables used in the analysis and their transformations are shown. Variables excluded due to high correlation values ($|r| \geq 0.8$) are displayed on the same row as the included variable with which they were correlated

Code	Included variables	Transformation	Excluded variables
NPP	Net primate productivity[1]	None	
ELEV	Elevation[2]	Log	
BIO1	Annual mean temperature[2]	None	Max temperature of warmest month[2], coldest month[2], wettest quarter[2], driest quarter[2], warmest quarter[2], coldest quarter[2]
BlO2	Mean diurnal temperature range [mean of monthly (max−min)][2]	Square root	Temperature annual range[2]
BlO3	Isothermality [(mean diurnal range/temperature annual range)*100][2]	Square root	Temperature seasonality[2] (SD*100)
BlO12	Annual precipitation[2]	None	
BlO13	Precipitation of wettest month[2]	Square root	Precipitation of wettest quarter[2]
BlO14	Precipitation of driest month[2]	Square root	Precipitation seasonality[2] (coefficient of variation); precipitation of coldest quarter[2], driest quarter[2]
BlO18	Precipitation of warmest quarter[2]	None	
T.SAND	Topsoil sand fraction[3]	Square root	Subsoil sand fraction[3], silt fraction[3], cation exchange capacity (soil)[3]; topsoil silt fraction[3], cation exchange capacity (soil)[3]
T.CLAY	Topsoil clay fraction[3]	Log	Subsoil clay fraction[3], reference bulk density[3], topsoil reference bulk density[3]
T.OC	Topsoil organic carbon'	Log	Subsoil organic carbon[3]
T.PH.H20	Topsail pH[3]	Square root	Topsoil base saturation[3], subsoil base saturation[3], pH[3]
T.CEC.CL	Topsoil cation exchange capacity (clay)[3]	Log	Topsoil total exchangeable bases[3]; subsoil total exchangeable bases[3], cation exchange capacity (clay)[3]

Sources: [1]Global Land Cover Facility (Carroll *et al.* 2009), [2]WorldClim Global Climate Database (Hijmans *et al.* 2005), [3]Harmonized World Soil Database [FAO/IIASA/ISRIC/IISSCAS/JRC (2009)].

through niche processes, then community similarity will be largely determined by ecological similarity: the species composition of communities inhabiting areas with similar ecological conditions will be more similar than those inhabiting more disparate ecological conditions, irrespective of geographical distance. Therefore, we test predictions emerging from two alternative hypotheses, following Chase *et al.* (2005):

H₁: Dispersal limitation determines the structure of primate communities
P₁ₐ: Negative correlation between community similarity and geographical distance
P₁ᵦ: No (or weak) correlation between community similarity and ecological distance
H₂: Niche differentiation through species sorting along environmental gradients determines the structure of primate communities
P₂ₐ: No (or weak) correlation between community similarity and geographical distance
P₂ᵦ: Negative correlation between community similarity and ecological distance

Materials and methods

COMMUNITY COMPOSITION DATA

Data for 124 sites across Africa ($N = 23$), South America ($N = 45$), Madagascar ($N = 28$) and Borneo ($N = 28$) were collected (Fig. 1). Primate community composition was assessed by compiling presence-absence data for species from published sources, following

Groves's (2001) taxonomy. See Appendix S1 for species and site information.

COMMUNITY SIMILARITY

The Jaccard community similarity index was calculated using the Vegdist function from the Vegan community ecology package in R (R Development Core Team 2009). The Jaccard index can be calculated with presence-absence or abundance data. For presence-absence data, the Jaccard index is defined as $JI = j/(a + b−j)$ where j is the number of species occurring in both sites, a is the number of species occurring in the first site and b is the number of species occurring in the second site (Magurran 1988). High values of the Jaccard community similarity index mean that two sites have high community similarity and thus a high number of species in common and few species found only at one site. The converse is true for low JI values.

GEOGRAPHICAL DISTANCE

Geographical coordinates were collected from the community composition site reference when available, or otherwise from the UNEP and IUCN Worldwide Database on Protected Areas (IUCN-UNEP 2009). Geographical distances were calculated using the Pairdist Function from the Sᴘᴀᴛꜱᴛᴀᴛ Package in R. For all pairs of sites within a region, Pairdist computes the matrix of Euclidean distances between latitude and longitude.

ECOLOGICAL DISTANCE

To determine ecological distance, 41 ecological variables (Table 1) were collected for each site from publically available datasets using ArcGIS. Excluding anthropogenic effects, it is likely that primate distributions are shaped primarily by the distributions of plant species
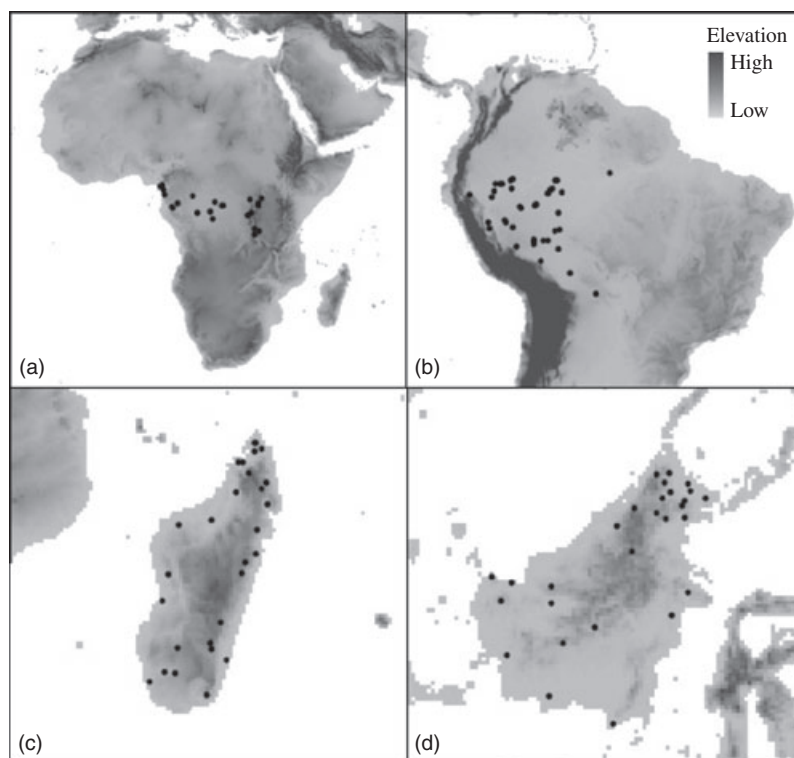
Fig. 1. Locations of primate communities. Map of primate community sites included in this study ($N = 124$) in (a) Africa ($N = 23$) (b) South America ($N = 45$) (c) Madagascar ($N = 28$) and d) Borneo ($N = 28$). Shading indicates elevation with high elevations displayed in dark grey. Squares indicate communities in which the most commonly found regional species was absent. There were no species found at all sites within any of the metacommunities. It is unlikely that this pattern is an artefact of the spatial scale at which we conducted this analysis because sites lacking the most common taxon in the regional metacommunity were not clustered together spatially, although this is less true for Africa where community composition is likely influenced by the Congo river. After conducting the analysis with all sites, we repeated our analysis using only sites where the most common species in each region was found in order to test our hypotheses where the assumption of metacommunity contiguity would be demonstrably valid. The presence of the same taxon at all sites demonstrates that all sites within the metacommunity have been accessible to dispersing individuals and therefore provides a more conservative test of the dispersal limitation hypothesis.

on which they feed. Although the debate remains ongoing, there is growing evidence that tropical plant distributions are largely determined by soil characteristics and topography (Potts *et al.* 2002; Russo *et al.* 2008). We therefore collected information on a wide range of ecological variables including net primary productivity, elevation, temperature, precipitation and soil characteristics in an attempt to assess factors that affect plant distributions (Franklin 1995). When two variables were highly correlated ($|r| > 0.8$) one was discarded from the data set prior to analysis by removing the variable that was believed to be less likely to affect primate ecology (Table 1). The remaining 14 ecological variables were used to calculate a matrix of ecological distances between each pair of primate community sites. As ecological values were correlated, we used a Mahalanobis distance calculation that would accommodate this correlation (Seber 1984). The Mahalanobis distance calculation is best performed with variables that have normal distributions. As ecological data are rarely normally distributed, the distributions of ecological variables were transformed when needed to stabilize their variances and make their distributions more symmetrical and therefore more normally distributed (Table 1). These analyses were conducted in R 2.8.1 (R Development Core Team 2009).

Ecological variation within and among regions was compared with a MANOVA using the 14 transformed ecological variables as response variables to the four regions. We tested for significant differences between all regions using six contrasts and a Bonferroni correction for the α = 0·05 level ($P = 0.008$). Ecological variation among

regions was illustrated using a canonical centroid plot and within regions by plotting 99% density ellipses for each region on a bivariate plot of canonical axes 1 and 2. These analyses were conducted in JMP 8.0.1 (SAS Institute Inc., Cary, NC).

ANALYSES

There has been substantial academic debate over the appropriate statistical methods, particularly Mantel tests and CCA, for testing the relative importance of spatial and ecological drivers of community composition. The crucial distinction reached in this debate is that CCA is appropriate for questions concerning variation in community composition, also known as beta diversity, whereas Mantel tests are appropriate for questions concerning variation in beta diversity between groups of sites (Legendre, Borcard & Peres-Neto 2005, 2008; Tuomisto & Ruokolainen 2006, 2008). As we are interested in the factors driving the variation in community composition across regions (i.e. dispersal limitation and species sorting along environmental gradients), we are interested in comparing the variation in beta diversity across sites; Mantel tests are therefore an appropriate statistical tool. It is important to note, however, that a major difference between Mantel tests and CCA is that when distances are calculated in the Mantel approach, the species identities, the actual values of the geographical coordinates of the sites and the actual values of the environmental values at the sites are no longer compared, but what is compared is the magnitude of the differences between them in

the form of 'distances'. CCA, on the other hand, quantifies the effects of the specific location on individual species at a site and does not quantify the effect of distances between sites on variation in community composition (Tuomisto & Ruokolainen 2006).

Simple Mantel tests were therefore performed to investigate bivariate correlations of community similarity with ecological distance and geographical distance. Partial Mantel tests (Smouse, Long & Sokal 1986) were employed to investigate partial relationships between these variables. These tests were performed in R using the 'mantel' and 'mantel.partial' commands, the Pearson method and 10 000 permutations. A similarity matrix was used for community composition and dissimilarity matrices were used for ecological and geographical distance. The R code for these analysis can be found in Appendix S2.

Added variable plots (Weisberg 1985) were constructed to depict the correlation values of the partial Mantel tests. To illustrate the influence of ecological distance on primate community similarity while controlling for geographical distance, diurnal community similarity was regressed against geographical distance, and 'community similarity residuals' were calculated based on the regression line. Ecological distance was regressed against geographical distance, and the resulting 'ecological distance residuals' were calculated. We then plotted the community residuals against the ecological residuals and calculated the corresponding regression line for each metacommunity. Similarly, the effects of ecological distance were partialled out to illustrate the effects of geographical distance on community similarity. The correlation coefficient for the points in each added variable plot is equal to the partial correlation coefficient having corrected for the partialled out predictor. The slope of the regression line through each added variable plot is equal to the coefficient that the respective predictor would have in a multiple regression model that included the other predictor.

Results

COMMUNITY COMPOSITION

There was considerable variation in the total number of diurnal species, nocturnal species and genera between the regional species pools (Table 2). There were no species found at all sites within any of the metacommunities. It is unlikely that this pattern is an artefact of the spatial scale at which we conducted this analysis because sites lacking the most common taxon in the regional metacommunity were not clustered together spatially (Fig. 1), although this is less true for Africa where communities are likely affected by the Congo river. The species most frequently present in each region were *Pan troglodytes* and *Perodicticus potto* present in 70% (16/23) of African sites, *Cebus apella* present in 93% (42/45) of South American sites, *Eulemur fulvus* present in 86% (24/28) of Malagasy sites and *Hylobates muelleri* present in 79% of (22/28) Bornean sites. We list site information and species found in each region in Appendix S1.

Table 2. Summary data for regional species pools

Taxa	Africa	South America	Madagascar	Borneo
Diurnal species	35	28	13	11
Nocturnal species	9	3	16	2
Genera	17	13	14	8

ECOLOGICAL DISTANCE

There were significant differences in ecology among all regions (MANOVA whole model Wilks' Lambda: $DF_{num} = 42$, $DenDF = 318.18$, $P < 0.0001$; Region contrasts: $N = 124$, $NumDF = 14$, $DF_{den} = 107$, $P < 0.0001$, Exact F: Madagascar – Borneo = 55.95, Madagascar – Africa = 40.92, Madagascar – South America = 39.70, South America – Borneo = 15.66, South America – Africa = 13.05, Borneo – Africa = 6.23). Madagascar is differentiated from the other three regions by the first canonical axis, which is largely explained by elevation and precipitation in the warmest quarter. South America is differentiated from the other three regions by the second canonical axis, which is largely explained by the topsoil properties pH, sand fraction and per cent organic carbon. Africa and Borneo are the most ecologically similar regions (Fig. 2a). Madagascar's larger density ellipse illustrates its greater within-region variation than the other regions (Fig. 2b). Regional summary statistics (minima, maxima and medians) for the 14 ecological variables included in the analyses are provided in Table S1.

MANTEL TESTS

The results of the simple Mantel tests show that geographical distance was a stronger predictor of community similarity than ecological distance in diurnal primate communities in Africa, South America and Borneo, but not in Madagascar (Table 3). Thus, sites that are geographically farther from each other have fewer species in common than sites that are geographically closer to each other. These results suggest that dispersal limitation affects primate community composition more than niche differentiation affects primate community composition in Africa, South America and Borneo, but not in Madagascar. We found the same pattern when we performed the analyses using all species.

When we performed the simple Mantel tests using genera, we found that geographical distance was a stronger predictor of community similarity in Africa and South America, but not in Madagascar or Borneo. These results suggest that dispersal limitation is a stronger predictor of primate community composition at the generic level in Africa and South America, but not in Madagascar or Borneo. Contrary to predictions of both hypotheses, community similarity in Borneo was more strongly predicted by a positive relationship with ecological distance. This result suggests that primate communities in Borneo at the genus level are more similar the more dissimilar the environments are.

The partial Mantel results were qualitatively the same as the simple Mantel results (Table 3). Importantly, these patterns remained consistent once the potentially confounding effects of spatial and environmental autocorrelation were removed. Geographical distance was a stronger predictor of community similarity than ecological distance in diurnal primate communities in Africa, South America and Borneo, but not in Madagascar (Table 3). These results indi-
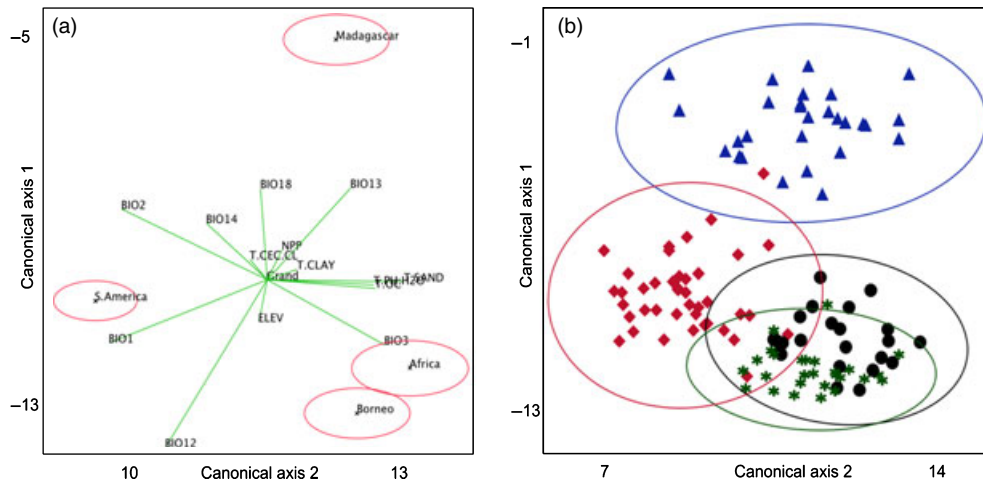
Fig. 2. Ecological variation between and within regions. (a) Canonical centroid plot depicting ecological variation between regions. Regional centroids are indicated by the × marks within ovals. The biplot rays show the direction and strength of the ecological variables responsible for the canonical axes. Variable codes correspond to variables described in Table 1. Madagascar is differentiated from the other three regions by the first canonical axis, which is largely explained by elevation and precipitation in the warmest quarter. South America is differentiated from the other three regions by the second canonical axis, which is largely explained by the topsoil properties pH, sand fraction and per cent organic carbon. Africa and Borneo are the most ecologically similar regions. (b) Ecological variation within regions as shown by 99% density ellipses. Malagasy sites are represented by blue triangles. South American sites are represented by red diamonds. African sites are represented by black circles. Bornean sites are represented by green asterisks. Madagascar's larger density ellipse illustrates its greater within-region variation than the other regions, which is one possible explanation for why the niche differentiation hypothesis of species sorting along environmental gradients is strongly supported in Madagascar, but not in the other three regions.

Table 3. Simple and partial Mantel tests of primate community similarity against ecological and geographical distance

Distance	Community	Africa		South America		Madagascar		Borneo	
		r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Geographic	Diurnal species	**−0·64**	**< 0·001**	**−0·37**	**< 0·001**	**−0·31**	**< 0·001**	**−0·29**	**0·001**
	All species	**−0·65**	**< 0·001**	**−0·36**	**< 0·001**	**−0·28**	**< 0·001**	**−0·22**	**0·007**
	Genera	**−0·55**	**< 0·001**	**−0·25**	**0·007**	**−0·27**	**< 0·001**	−0·04	0·64
Ecological	Diurnal species	**−0·26**	**< 0·001**	**−0·19**	**0·025**	**−0·33**	**< 0·001**	−0·11	0·152
	All species	**−0·30**	**< 0·001**	**−0·21**	**0·014**	**−0·43**	**< 0·001**	−0·06	0·306
	Genera	**−0·43**	**< 0·001**	**−0·20**	**0·043**	**−0·32**	**< 0·001**	+0·07	0·724
Geographical (Ecological partialled out)	Diurnal species	**−0·61**	**< 0·001**	**−0·33**	**< 0·001**	**−0·25**	**< 0·001**	**−0·27**	**< 0·001**
	All species	**−0·61**	**< 0·001**	**−0·30**	**< 0·001**	**−0·22**	**0·004**	**−0·22**	**0·002**
	Genera	**−0·48**	**< 0·001**	**−0·17**	**0·029**	**−0·22**	**0·002**	+0·01	0·543
Ecological (Geographical partialled out)	Diurnal species	**−0·07**	**0·032**	+0·01	0·533	**−0·28**	**< 0·001**	<−0·01	0·524
	All species	**−0·13**	**0·025**	−0·02	0·37	**−0·39**	**< 0·001**	+0·04	0·638
	Genera	**−0·32**	**0·002**	−0·08	0·232	**−0·27**	**0·005**	+0·06	0·709

Correlation values (*r*) and significance values (*P*) are given for each test for primate communities in Africa, South America, Madagascar and Borneo. Communities were defined using diurnal species, all species or genera. Results significant at the α ≤ 0·05 level are indicated in bold. The stronger predictor (i.e. greater absolute correlation value and equal or smaller *P*-value) is shaded in grey for each comparison between geographical and ecological results from each simple and partial test in each region at each community level. Of 24 comparisons, 16 support hypothesis 1 and reject hypothesis 2 and no comparisons support hypothesis 2 fully, suggesting that neutral mechanisms are important determinants of primate community structure and may play a stronger role in shaping primate community structure than niche mechanisms.

cate that sites that are geographically farther from each other have fewer species in common than sites that are geographically closer to each other even once differences in ecology are removed. These results suggest that dispersal limitation affects primate community composition more than niche differentiation affects primate community composition in Africa, South America and Borneo, but not in Madagascar. We illustrated the partial Mantel results for diurnal primate communities using added variable plots (Fig. 3).

The results of the partial Mantel tests differed from the simple Mantel tests in two ways. First, the correlation values of the simple tests were consistently higher. This indicates that removing the spatial and environmental autocorrelation with the partial Mantel tests weakened the relationships between primate community similarity and ecological distance and between primate community similarity and geographical distance. Secondly, the correlation between community similarity and ecological distance was non-significant for South America after partialling out geographical distance.
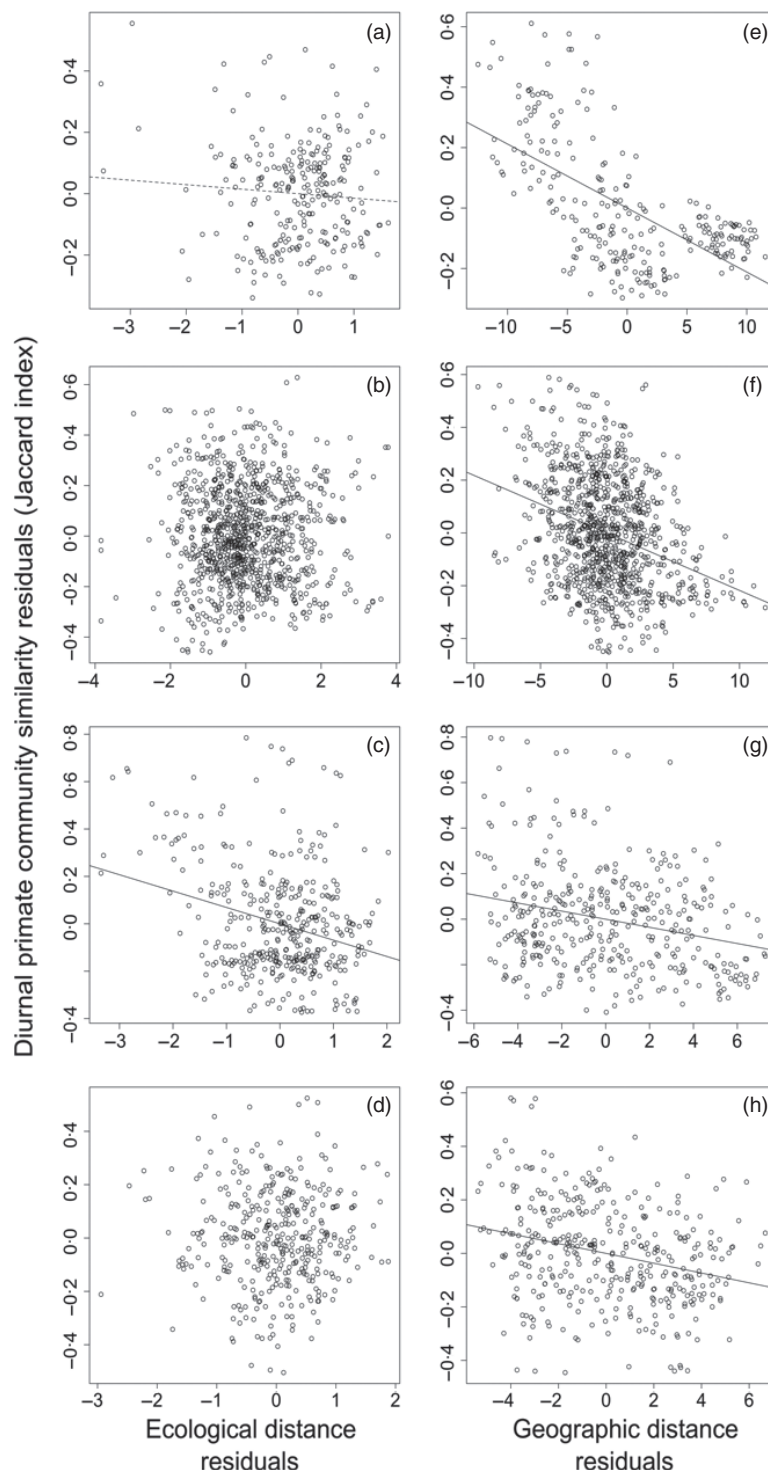
Fig. 3. Added variable plots depicting correlation values of partial Mantel tests for diurnal primate communities. We plotted community residuals against ecological residuals for (a) Africa (b) South America (c) Madagascar and (d) Borneo. We plotted community residuals against geographical residuals for (e) Africa (f) South America (g) Madagascar and (h) Borneo. When $\alpha = 0.05$, ecological distance is only significantly correlated with diurnal community similarity in Africa ($r = 0.03$) and Madagascar but geographical distance is significantly negatively correlated with diurnal community similarity in metacommunities from all regions (Table 3). These results support the hypothesis that dispersal limitation structures primate communities in all regions. For Madagascar, and very weakly for Africa, there is also support for the hypothesis that niche differentiation through species sorting along environmental gradients structures primate communities.

Nevertheless, despite removing the effects of the spatial autocorrelation, Africa and Madagascar maintained significant relationships between primate community similarity and ecological distance. These results suggest that niche differentiation may significantly affect primate community structure in Africa and Madagascar, although the strength of the

relationship in Africa is very low ($r = 0\cdot07$). Given the recent statistical debate over the merits of statistical significance and *P*-values (Hurlbert & Lombardi 2009), we believe that the effect sizes or in this case the correlation values are better indicators of the results than the significance values. Therefore, although there is a significant negative relationship between community similarity and ecological distance in Africa, the small effect size suggests that the biological significance of the relationship is minor.

Model summaries for the multiple regression models for community similarity with ecological distance and geographical distance as predictors are Africa, $N = 253$, $R^2 = 0\cdot41$; South America, $N = 990$, $R^2 = 0\cdot14$; Madagascar, $N = 378$, $R^2 = 0\cdot17$; Borneo, $N = 378$, $R^2 = 0\cdot08$. The number of observations in the pairwise distance matrix (N) for each metacommunity is $N = n*(n-1)/2$ where n is equal to the number of primate community sites per metacommunity. The R^2 values can be interpreted as the percent of variance in community similarity explained by the two distance measures. We therefore were able to explain the most variance for Africa (41%), intermediate levels for South America (14%) and Madagascar (17%) and the least variance for Borneo (8%).

To assess the extent to which our choice of community similarity index affected the results of the Mantel tests, we repeated our analyses using an alternative similarity index, the Sørensen Index. Similarly, to assess the extent to which our choice of ecological variables affected the results of the Mantel tests, we repeated our analyses using a set of 19 variables from the overall database of 41 variables. In both cases, additional analyses produced qualitatively similar results in that the relative importance of dispersal limitation and niche differentiation remained unchanged in each of the regions (Table S2).

To evaluate whether individual ecological variables become buried in the ecological distance matrix, we examined scatter plots of ecological dissimilarities between pairs of sites vs. raw differences in ecological variables (Appendix S3). The plots show that as pairwise differences in a given ecological variable deviate from zero (positively or negatively), the corresponding Mahalanobis distances between pairs of sites tend to increase. Large Mahalanobis distances occurring near the zero value of the horizontal axis are the result of differences between sites with respect to other ecological variables. As the plots show that when pairwise differences for each ecological variable are large, the Mahalanobis distance value is also large, they therefore show that the effects of individual ecological variables are not buried in the ecological matrix.

Discussion

We found significant and stronger negative relationships between community similarity and geographical distance than between community similarity and ecological distance in Africa, South America and Borneo. In Madagascar, we found significant negative relationships between community similarity and geographical distance as well as community similarity and ecological distance. These results support both predictions from H1 for Africa, South America and Borneo and fail to support both predictions from H2 for Madagascar. The same pattern occurred when we included nocturnal species and to a lesser extent when we conducted the tests at the generic level. Overall, 16 of 24 comparisons are consistent with H1 but not H2, and no comparison fully supports H2 (Table 3). These results suggest that dispersal limitation is an important determinant of primate community structure and may play a stronger role in shaping primate community structure than niche mechanisms, such as species sorting along environmental gradients.

Although we detected patterns consistent with dispersal limitation across regions, dispersal limitation explains only a subset of the variance (Fig. 3). A more refined model would include relative species abundances, speciation rates, species-specific maximum dispersal distances, the influence of geographical barriers on dispersal and indices of human disturbance. Our analyses do not explicitly address phylogeography, historical climates, primate diets, non-primate competitors, or human impacts. Detailed modelling that parses out the relative influence of such factors would provide a better understanding of primate community assembly; however, a lack of sufficient data across species and sites constrained our analysis.

We also caution that without experimental evidence it is possible that mechanisms other than dispersal limitation could have produced similar patterns (for review, see Alonso, Etienne & McKane 2006). In addition, it has previously been pointed out that failure to find correlations with environmental variables may simply reflect failure to incorporate the appropriate environmental variables (Bell, Lechowicz & Waterway 2006). Moreover, relevant variables may include biotic rather than abiotic variables. Lastly, we recognize that ecological factors may vary in their importance for primates among regions. We used the same ecological distance matrix across regions so that results would be comparable, but future tests within regions would benefit from model selection approaches.

Although primates are highly mobile and capable of travelling substantial distances, many species restrict their activities to areas of well-known forest for efficient exploitation (Fleagle 1999). Moreover, primate dispersal is costly for reasons such as exposure to higher predation risk, loss of knowledge about local food resources and loss of benefits of remaining near kin (Isbell & van Vuren 1996). Colonization of new areas might impose similar costs. Dispersal and recruitment limitation may therefore influence primate community assembly, as has been found for sessile taxa (Hubbell 1997).

We detected a stronger signal of dispersal limitation when nocturnal primate species were excluded from the partial Mantel analyses. This difference may be due to sampling biases against detecting cryptic nocturnal species. Alternatively, solitary nocturnal species may experience lower dispersal costs and therefore reduced dispersal limitation in comparison with group living diurnal species. For example,

their anti-predator strategies involve crypsis and solitary living, which may cause them to be less dependent than gregarious diurnal taxa on dispersing with other individuals. However, despite the large difference in the proportion of nocturnal primates (Table 2), we do not see a response in the dispersal limitation signal that is proportional to the number of nocturnal primates across regions.

Like the other three regions, Malagasy community structure was strongly predicted by geographical distance, which suggests that dispersal limitation is an important factor. Unlike the other three regions, however, ecological distance was a stronger predictor. Interestingly, a recent study of primate community phylogenetics found that a majority of primate communities from Africa, South East Asia and the Neotropics exhibit random phylogenetic structure, but that Malagasy communities tend to be overdispersed, such that species within these communities are less closely related to each other than is expected by chance (Kamilar & Guidi 2010). These findings are consistent with the idea that competition between closely related species in the past may have resulted in their competitive exclusion (Webb *et al.* 2002). The results of our study as well as the community phylogenetics study (Kamilar & Guidi 2010) suggest that competition may be a more important mechanism structuring primate communities in Madagascar than in other regions. One possible explanation is that primates in Madagascar represent a larger portion of the appropriate vertebrate competitor community and therefore the effects of niche differentiation were more readily detected. In Madagascar, primates compose 44% of the nonvolant terrestrial mammals, whereas in other regions primates compose 8–12% (Jernvall & Wright 1998). If non-primate competitors are more important than primate competitors, the effects of niche differentiation in other regions may be masked by their exclusion. Alternatively, the stronger ecological result in Madagascar may be attributable to greater ecological variation within the region (Fig. 2b).

Geographical barriers, such as mountain ranges, rivers and forest discontinuities may have affected primate dispersal. It is unlikely that mountain ranges posed major geographical barriers for these sites (Fig. 1), but major rivers are found in all four regions. Although the role of rivers as dispersal barriers to primates has received support (Ayres & Clutton-Brock 1992; Jalil *et al.* 2008), others have questioned the extent to which rivers are complete barriers (Oates 1988; Gascon *et al.* 2000). The presence of a negative non-linear relationship between African primate community similarity and geographical distance (Fig. 3e) may be attributable to the Congo River, which serves as a barrier to the distribution of some primates. Primate communities to the east and west of the Congo Basin may contain species that have dispersed without crossing the Congo River. Past or present forest cover discontinuities may also have hindered primate dispersal (Grubb 1982), but riverine forests may have functioned as dispersal corridors, particularly in Africa and Madagascar (Colyn, Gautier-Hion & Verheyen 1991; Ganzhorn *et al.* 2006). Although geographical barriers may be the

reason why no species was found at all sites within a region, the high proportion of sites occupied by the most frequently found species per region suggests that most sites within a region could potentially be reached. Moreover, when we repeated analyses using only sites at which the most common regional species was present, we found the same qualitative results in that the relative importance of dispersal limitation and niche differentiation remained unchanged in each of the regions (Table S2). These findings suggest that dispersal limitation has shaped primate community structure beyond the effects of geographical barriers, although detailed modelling of the effects of geographical barriers on species distributions would provide further insight into mechanisms of primate dispersal limitation.

Neutral models have been applied to vertebrate communities surprisingly rarely and the few studies to date have produced mixed results (McGill 2003; He 2005; Ostling 2005; Muneepeerakul *et al.* 2008). Our findings are consistent with neutral theory and warrant further exploration. Hubbell's (2001) neutral model considers all members of a trophic community to be functionally equivalent. Testing the validity of the functional equivalence hypothesis will be central to determining the extent to which neutral theory may explain primate community composition.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Site information and regional species pools for all regions.

Appendix S2. R code for statistical analyses.

Appendix S3. Effects of individual ecological variables on ecological distance matrix calculated using Mahalanobis distance.

Table S1. Summary statistics for ecological variables used in the analyses.

Table S2. Mantel results using (a) Jaccard Index and 19 ecological variables (b) Sørensen Index and 14 ecological variables (c) sites at which the most common regional species is found.

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