

# African Primate Assemblages Exhibit a Latitudinal Gradient in Dispersal Limitation

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**Abstract** Recent studies have demonstrated that dispersal limitation, which refers to the limited ability of individuals to reach distant geographic areas, is an important influence on the species that are found in primate assemblages. In this study, we investigate the relative influences of dispersal limitation and environmental filtering in 131 African primate assemblages in 9 biogeographic regions throughout sub-Saharan Africa. Specifically, we evaluate the dispersal-ecological specialization hypothesis, which posits that there are trade-offs between dispersal ability and ecological specialization that are influenced by climatic variation along latitudinal gradients. The hypothesis predicts that species in assemblages near the equator, where climatic conditions are more stable, will exhibit stronger dispersal limitation and greater ecological specialization than species within assemblages located further from the equator, where climate is more variable. In contrast, assemblages located at higher latitudes are expected to be influenced more strongly by environmental filtering than dispersal

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limitation. We used hierarchical cluster analysis to identify regions, conducted partial Mantel tests to evaluate the contributions of dispersal limitation and environmental filtering in each region, and evaluated predictors of those contributions with linear regression. In all regions, dispersal limitation was a stronger predictor of community similarity than was environmental filtering, yet the strength of dispersal limitation varied. Dispersal limitation was greatest at low latitudes and declined with increasing absolute latitude. Thus, primate assemblages exhibited a significant latitudinal gradient in dispersal limitation, but not in environmental filtering. These results support aspects of the dispersal-ecological specialization hypothesis and call for future mechanistic studies to address this broad-scale pattern.

**Keywords** Biogeography · Community assembly · Gene flow · Macroecology · Metacommunity · Niche · Primate communities

## Introduction

Understanding the mechanisms that govern the assembly and maintenance of ecological communities is a central question in ecology. A major focus in the field of community ecology since the emergence of neutral theory (Hubbell 2001) has been to disentangle the relative importance of dispersal limitation and niche mechanisms for determining community composition, which is the species composition of groups of organisms living together. Dispersal limitation occurs when a species that is present in the regional species pool and that would be able to persist at a site given the environmental conditions is absent because individuals of the species are limited in their ability to reach the site and persist (Hubbell 2005). If dispersal limitation is more important than environmental characteristics for structuring communities, then sites that are spatially close together are expected to share many species; community similarity is expected to decrease with increasing geographic distance. In contrast, if the environment determines community similarity then sites with similar habitat or climate conditions are expected to share more species irrespective of the geographic distance between sites (hereafter “environmental filtering”); community similarity is expected to decrease with increasing environmental distance (Chase *et al.* 2005). These scenarios are not mutually exclusive but a comparison can reveal the relative strengths of environmental and geographic influences.

The *dispersal-ecological specialization hypothesis* posits that trade-offs between species’ dispersal ability and ecological specialization drive latitudinal patterns of species richness (Jocque *et al.* 2010). This latitudinal effect is ultimately linked to local climate and habitat characteristics, which are more stable in the tropics, thus allowing for specialization, and more seasonal at higher latitudes, thus requiring greater dispersal abilities and ecological flexibility. Under this hypothesis, on one end of the continuum are harsh, highly seasonal climates as found at higher latitudes. Harsh climates are predicted to favor high dispersal because dispersal allows organisms to respond to climatic variability (Gandon and Michalakis 2001). High dispersal results in high gene flow, which causes low isolation and thus low speciation rates and low overall species diversity. At the other end of the continuum are less harsh, less seasonal climates, such as the tropics, which are hypothesized to have reduced selective pressure for dispersal

because greater environmental stability reduces the need for an organism to track its preferred resources and environmental conditions (Jocque *et al.* 2010). Greater environmental stability therefore allows for greater ecological specialization because resource availability is more stable. Ecological specialization in turn results in low gene flow because the probability of an organism finding preferred conditions is highest in nearby locations. Low gene flow results in high isolation, high speciation rates, and consequently high species diversity. Some models predict that extinction rates are higher in the tropics than temperate areas when species with narrow ranges are eliminated disproportionately by catastrophic environmental change (Arita and Vazquez-Dominguez 2008) while other models do not (Weir and Schluter 2007). Speciation rates are expected to be higher in the tropics and thus overall species richness increases through time when speciation rates exceed extinction rates (Jocque *et al.* 2010). Under conditions put forth by the dispersal-ecological specialization hypothesis, dispersal limitation is predicted to be greater in tropical communities than in communities at latitudes further from the equator.

A meta-analysis of more than 400 studies found that large-bodied, terrestrial, mobile organisms generally exhibit low dispersal limitation (Soininen *et al.* 2007). However, fewer than 3 % of the studies used in this meta-analysis were from tropical regions and none of these tropical studies were of mammals. Moreover, several studies have found that dispersal limitation significantly affects tropical forest primate communities (Beaudrot and Marshall 2011; Beaudrot *et al.* 2013; Gavilanez and Stevens 2013; Kamilar 2009). In each case, researchers showed that geographic distance was a significant predictor of community composition, even after controlling for spatial autocorrelation in ecological conditions. In addition, other recent studies of tropical plant and animal communities have suggested that latitudinal gradients in dispersal ability may occur (Leithead *et al.* 2012; Munguia *et al.* 2008).

**Table 1** Summary of biogeographic regions used in the analysis of dispersal limitation and environmental filtering

ID	Name	Latitude mean	N sites	Area (km <sup>2</sup> )	Environmental variation (MCP area)	Species richness		
						Region total	Site min	Site max
1	Guinean	9.55	8	803,001	10.37	19	7	14
2	Nigerian	11.19	27	1,448,431	6.44	13	4	9
3	Ethiopian	8.35	5	278,342	9.48	8	4	6
4	Congolian	0.96	19	1,244,383	4.95	38	7	17
5	Lake Tanganyikan	-2.62	12	64,835	12.73	24	9	20
6	E. African	-3.42	26	1,386,628	35.53	23	4	12
7	W. Zambezan	-11.30	6	246,141	1.82	9	4	7
8	E. Zambezan	-14.69	10	248,054	3.78	6	5	6
9	South African	-20.30	18	1,647,339	20.74	7	4	6

Region ID values correspond to numerical labels in Fig. 1. For each region we list the mean latitude, the number of sites, the area, the regional environmental variation, the total species richness of the region, and the minimum and maximum species richness of sites within a region. Study site: Africa; taxa: all primates.

Given the fact that primates are generally considered tropical species, are mobile animals (as opposed to sessile organisms), and exhibit relatively large body sizes, their dispersal limitation is unexpected and raises a number of important questions. In particular, are assemblages of primates consistently influenced by dispersal limitation across latitudes or is the documented dispersal limitation of primates reflective of their tropical distributions? African primates serve as a good test of this question because most species are found in tropical regions, yet primates also exist in higher absolute latitudes that exhibit more variable climatic conditions.

We assess the relative influence of dispersal limitation on primate assemblages across continental Africa and evaluate the effects of absolute latitude on dispersal limitation in order to evaluate the dispersal-ecological specialization hypothesis. The hypothesis predicts that dispersal limitation will be strongest at the equator and decline as absolute latitude increases. Alternatively, the relative importance of dispersal limitation may also change across spatial scales (Cavender-Bares *et al.* 2009; Chase and Myers 2011) and thus variation in the spatial extent of different biogeographic regions could also drive such a latitudinal gradient. We therefore evaluate the relationship between regional spatial extent and dispersal limitation. A significant relationship between geographic area and dispersal limitation would suggest that these processes are related to spatial scaling rather than trade-offs in dispersal ability and specialization, as predicted by the dispersal-ecological specialization hypothesis.

## Methods

### Data Compilation

We compiled presence–absence data for African primate assemblages from published sources (Electronic Supplementary Material [ESM] Appendix S1). Our dataset was collected as part of a larger project focused on a variety of macroecological and macroevolutionary questions (Kamilar *et al.*, this issue). We employed a taxonomy that was based on GenBank, following the 10 K Trees primate phylogeny (Arnold *et al.* 2010). Recent broad-scale studies of primate communities have shown that taxonomic scheme has a minimal effect on results (Kamilar and Guidi 2010). We excluded sites with fewer than four primate species (ESM Appendix S2) because some measures of community similarity can be affected by very low species richness. We analyzed primate assemblages from 134 sites across Africa, which included a total of 59 primate species.

### Identification of Biogeographic Regions

Statistical methods have been developed for identifying biogeographic regions based on identifying clusters of sites with broadly similar species composition (Holt *et al.* 2013; Kreft and Jetz 2010; Linder *et al.* 2012). Clustering algorithms reduce the likelihood of including prohibitively strong dispersal barriers or starkly different environments sharing few to no species in common. Clustering therefore provides biologically meaningful regions within which to investigate the drivers of community composition (Carstensen *et al.* 2013).

We assigned study sites into biogeographic regions based on hierarchical cluster analysis conducted with the “recluster” package in R (Dapporto *et al.* 2013a). This clustering method creates consensus trees, which result in stronger biogeographic region delineations than are produced by single-tree approaches conducted without resampling techniques because results of single-tree approaches are biased by the site order of the input data matrix (Dapporto *et al.* 2013a). We determined consensus trees by first shuffling the order of sites from the data matrix and then repeatedly resampling from the shuffled data. A multiscale bootstrap analysis quantifies the percentage of trees representing the original node, and thus the certainty with which nodes are recovered (Dapporto *et al.* 2013a). Because there were many nodes for which the percentage of times in which the node was recovered was low, we followed the published guidelines and used a 50 % consensus value for creating consensus trees (Dapporto *et al.* 2013a). We used the `recluster.multi` function with the unweighted pair group method with arithmetic mean (UPGMA) clustering method and 1000 bootstrap iterations (Dapporto *et al.* 2013b). UPGMA calculates the mean distance between clusters as the distance between each cluster point and all other points in a different cluster. A new cluster forms from the two clusters with the lowest mean distance (Fielding 2007). A recent quantitative comparison of clustering methods demonstrated that the UPGMA method performed best when comparing results across taxonomic levels, i.e., family, genus, species (Kreft and Jetz 2010).

We conducted the cluster analysis using the Sørensen community similarity index because this index is one of the most widely used indices in ecological studies, therefore making our results comparable to previous work. We also conducted clustering with the  $\beta_{sim}$  index because this index is independent of species richness (Baselga *et al.* 2007) and found that the dendrograms produced comparable biogeographic regions, which suggests that the determination of biogeographic regions using the Sørensen index was not based on species richness.

We then employed the following rules for identifying biogeographic clusters from the consensus tree: 1) Regions could not be nested within each other (Linder *et al.* 2012), which excluded some sites from assignment into a region. 2) If an unassigned site was spatially located within or was the geographically closest site to an otherwise defined biogeographic region, we assigned the site to the region. 3) If a site remained unassigned, we excluded it from analysis ( $N=3$ ).

### Partial Mantel Tests

We used partial Mantel tests (Smouse *et al.* 1986) with the Pearson method and 10,000 randomizations to investigate the relative influence of environmental distance and geographic distance for predicting primate community similarity within each biogeographic region. Environmental and geographic distance matrices were the predictor variables and a community similarity matrix was the dependent variable.

We measured community similarity using the Sørensen index (Magurran 1988). In addition, we also evaluated predictors of community similarity, i.e., environmental distance and geographic distance, based on the  $\beta_{sim}$  index (Baselga 2007) for the reasons described previously.

Because we sought to evaluate the effects of climate variability on primate community composition across regions, we defined environmental filtering and thus

environmental distances between sites based only on climatic variables. Environmental distances included four climate variables selected to encapsulate climatic variability across continental Africa: mean annual precipitation, mean annual temperature, precipitation seasonality (coefficient of variation), and temperature seasonality (standard deviation \* 100). Using geographic coordinates, we extracted climate data at a 2.5 arc-minutes resolution from the Worldclim database (Hijmans *et al.* 2005) with ArcGIS. We calculated the pairwise environmental distances between all sites in each region using a Mahalanobis distance, which accounts for collinearity among variables in a manner analogous to principal components analysis (Seber 1984).

We measured geographic distance, or the spatial distance between all pairs of sites in a region, with a Euclidean distance calculation.

### Dispersal Limitation Signal

We used a commonly employed proxy to estimate dispersal limitation: the extent to which the straight-line distance between sites predicted similarity in species composition. Specifically, we measured the dispersal limitation signal using the partial Mantel correlation coefficient ( $r$ ), which is the correlation coefficient produced by the regression of community similarity residuals on geographic distance residuals after environmental distance has been regressed on these two matrices. We interpret higher absolute values of this correlation to indicate that dispersal limitation has a more important role in structuring community similarity.

### Predictors of Dispersal Limitation and Climate Variability

We used linear regression to determine if the strength of dispersal limitation, i.e., the effect size, was greater in regions with larger areas. This model included the mean absolute latitude of each biogeographic region as a predictor and the regional area as the dependent variable. We quantified the regional area, which is the spatial extent of each region, using the `earth.poly` function from the `fossil` package in R (Vavrek 2011) by calculating the minimum convex polygon surrounding all sites in a region.

We used linear regression to determine if the strength of dispersal limitation varied across latitude. This model included the mean absolute latitude of each biogeographic region as a predictor and the dispersal limitation signal as the dependent variable. Similarly, we used linear regression to determine if environmental variability within sites varied with absolute latitude. These models included the mean absolute latitude of each region as the predictor and 1) the median temperature seasonality as the dependent variable or 2) the median precipitation seasonality as the dependent variable.

We quantified the total amount of environmental variation for each region, i.e., variation between sites, as measured in this study by determining the area of the minimum convex polygon (MCP) surrounding the environmental variation of all sites in a region as displayed in a principal components analysis. We used the “`ordihull`” function in the “`vegan`” package in R to calculate the MCP area (Oksanen *et al.* 2013).

We conducted all analyses and created all figures using R version 3.0.0 (R Development Core Team 2013).

## Results

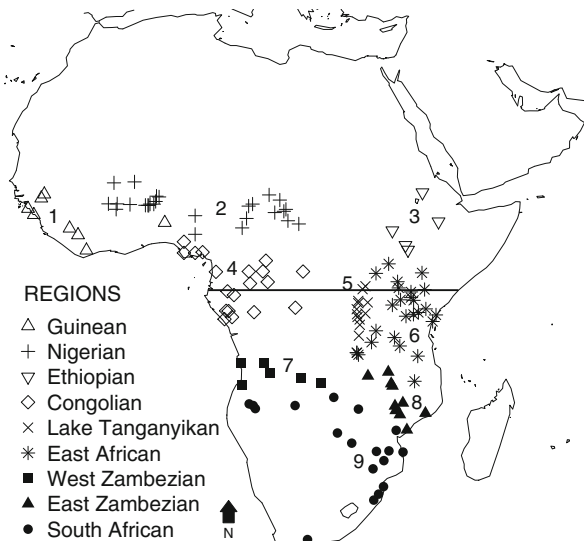
### Biogeographic Regions

The cluster analysis grouped African primate communities into nine biogeographic regions, which we refer to as the Guinean, Nigerian, Ethiopian, Congolian, Lake Tanganyikan, East African, West Zambezan, East Zambezan, and South African regions (Table I; Fig. 1). We provide species lists for each region (Table II). Clusters were well supported for the Guinean, Nigerian, Ethiopian, Congolian, Lake Tanganyikan, and South African regions. The Guinean, Ethiopian, and Congolian clusters had no additional sites manually assigned to them from other clusters and the Nigerian, Lake Tanganyikan, and South African clusters had two or fewer sites manually assigned. Clusters were less reliably retrieved for the other regions, particularly in the East African region, which combined two spatially overlapping clusters as well as additional manually assigned sites (ESM Appendix S3).

The amount of total environmental variability within each region varied considerably. The East African region contained the most variability between sites followed by the South African region. The regions with the least environmental variability between sites were the West and East Zambezan (Table I).

### Climatic Variability Across Regions

Mean absolute regional latitude significantly predicted median temperature seasonality (linear regression,  $R^2=0.90$ ,  $df=7$ ,  $P<0.01$ ) and median precipitation seasonality (linear regression,  $R^2=0.52$ ,  $df=7$ ,  $P=0.02$ ) across regions (Fig. 2). This



**Fig. 1** Map of 131 African primate assemblages with four or more primate species. Each of the nine biogeographic regions is represented by a unique symbol that corresponds to the region names. Numbers correspond to regions in Tables I and II. The equator is shown with a solid black line. Solid black symbols depict regions for which geographic distance did not significantly predict primate community composition.



**Table II** Regional species lists

<b>Region 1</b>	<b>Region 2</b>	<b>Region 3</b>	<b>Region 4</b>
<i>Cercocebus torquatus</i>	<i>Cercocebus galeritus</i>	<i>Cercopithecus mitis</i>	<i>Allenopithecus nigroviridis</i>
<i>Cercopithecus campbelli</i>	<i>Cercopithecus mona</i>	<i>Cercopithecus neglectus</i>	<i>Arctocebus aureus</i>
<i>Cercopithecus Diana</i>	<i>Cercopithecus neglectus</i>	<i>Chlorocebus aethiops</i>	<i>Arctocebus calabarensis</i>
<i>Cercopithecus mona</i>	<i>Cercopithecus nictitans</i>	<i>Colobus guereza</i>	<i>Cercocebus galeritus</i>
<i>Cercopithecus nictitans</i>	<i>Cercopithecus pogonias</i>	<i>Erythrocebus patas</i>	<i>Cercocebus torquatus</i>
<i>Cercopithecus petaurista</i>	<i>Chlorocebus aethiops</i>	<i>Papio anubis</i>	<i>Cercopithecus ascanius</i>
<i>Chlorocebus aethiops</i>	<i>Colobus guereza</i>	<i>Papio hamadryas</i>	<i>Cercopithecus cephus</i>
<i>Colobus polykomos</i>	<i>Colobus vellerosus</i>	<i>Theropithecus gelada</i>	<i>Cercopithecus dryas</i>
<i>Colobus vellerosus</i>	<i>Erythrocebus patas</i>		<i>Cercopithecus erythrogaster</i>
<i>Erythrocebus patas</i>	<i>Galago moholi</i>	<b>Region 7</b>	<i>Cercopithecus erythrotis</i>
<i>Galago senegalensis</i>	<i>Galago senegalensis</i>	<i>Cercopithecus ascanius</i>	<i>Cercopithecus mona</i>
<i>Galagoides thomasi</i>	<i>Papio anubis</i>	<i>Cercopithecus mitis</i>	<i>Cercopithecus neglectus</i>
<i>Galagoides demidoff</i>	<i>Procolobus verus</i>	<i>Chlorocebus aethiops</i>	<i>Cercopithecus nictitans</i>
<i>Pan troglodytes</i>		<i>Colobus angolensis</i>	<i>Cercopithecus pogonias</i>
<i>Papio anubis</i>	<b>Region 6</b>	<i>Galago moholi</i>	<i>Cercopithecus preussi</i>
<i>Papio papio</i>	<i>Cercocebus galeritus</i>	<i>Galagoides thomasi</i>	<i>Cercopithecus solatus</i>
<i>Perodicticus potto</i>	<i>Cercopithecus ascanius</i>	<i>Miopithecus talapoin</i>	<i>Chlorocebus aethiops</i>
<i>Ptilocolobus badius</i>	<i>Cercopithecus erythrotis</i>	<i>Otolemur crassicaudatus</i>	<i>Colobus angolensis</i>
<i>Procolobus verus</i>	<i>Cercopithecus mitis</i>	<i>Papio cynocephalus</i>	<i>Colobus guereza</i>
	<i>Cercopithecus mona</i>		<i>Colobus polykomos</i>
<b>Region 5</b>	<i>Cercopithecus nictitans</i>	<b>Region 8</b>	<i>Colobus satanas</i>
<i>Cercopithecus ascanius</i>	<i>Chlorocebus aethiops</i>	<i>Cercopithecus mitis</i>	<i>Colobus vellerosus</i>
<i>Cercopithecus hamlyni</i>	<i>Colobus angolensis</i>	<i>Chlorocebus aethiops</i>	<i>Euoticus elegantulus</i>
<i>Cercopithecus lhoesti</i>	<i>Colobus guereza</i>	<i>Galago moholi</i>	<i>Euoticus pallidus</i>
<i>Cercopithecus mitis</i>	<i>Colobus polykomos</i>	<i>Galago zanzibaricus</i>	<i>Galago senegalensis</i>
<i>Cercopithecus neglectus</i>	<i>Erythrocebus patas</i>	<i>Otolemur crassicaudatus</i>	<i>Galago alleni</i>
<i>Cercopithecus pogonias</i>	<i>Galago moholi</i>	<i>Papio cynocephalus</i>	<i>Galagoides thomasi</i>
<i>Chlorocebus aethiops</i>	<i>Galago senegalensis</i>		<i>Galagoides demidoff</i>
<i>Colobus angolensis</i>	<i>Galago zanzibaricus</i>	<b>Region 9</b>	<i>Gorilla gorilla</i>
<i>Colobus guereza</i>	<i>Galagoides demidoff</i>	<i>Cercopithecus mitis</i>	<i>Lophocebus aterrimus</i>
<i>Euoticus elegantulus</i>	<i>Lophocebus albigena</i>	<i>Chlorocebus aethiops</i>	<i>Lophocebus albigena</i>
<i>Galago matschiei</i>	<i>Otolemur crassicaudatus</i>	<i>Galago moholi</i>	<i>Mandrillus leucophaeus</i>
<i>Galago moholi</i>	<i>Otolemur garnettii</i>	<i>Galago zanzibaricus</i>	<i>Mandrillus sphinx</i>
<i>Galago senegalensis</i>	<i>Pan troglodytes</i>	<i>Otolemur crassicaudatus</i>	<i>Miopithecus talapoin</i>
<i>Galagoides thomasi</i>	<i>Papio anubis</i>	<i>Papio anubis</i>	<i>Pan paniscus</i>
<i>Galagoides demidoff</i>	<i>Papio cynocephalus</i>	<i>Papio ursinus</i>	<i>Pan troglodytes</i>
<i>Gorilla gorilla</i>	<i>Papio ursinus</i>		<i>Perodicticus potto</i>
<i>Lophocebus albigena</i>	<i>Ptilocolobus badius</i>		<i>Ptilocolobus badius</i>
<i>Otolemur crassicaudatus</i>			
<i>Pan troglodytes</i>			
<i>Papio anubis</i>			
<i>Papio cynocephalus</i>			



**Table II** (continued)

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<i>Perodicticus potto</i>
<i>Ptilocolobus badius</i>
<i>Ptilocolobus rufomitratus</i>

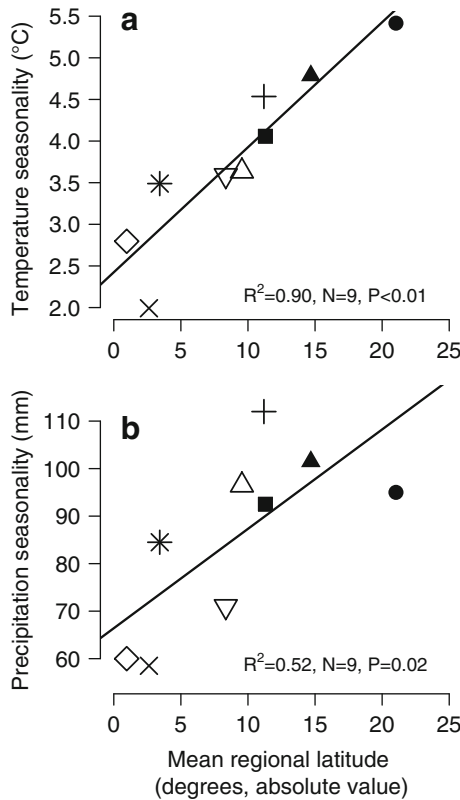
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Study site: Africa; taxa: all primates.

demonstrates that primate populations at sites in regions near the equator experience relative climatic stability while primate communities at sites in regions further from the equator experience greater climate variability.

**Partial Mantel Tests**

Geographic distance was a stronger predictor of primate community similarity than environmental distance in all regions based on an examination of the partial Mantel correlation coefficients (*r*) (Table III). Geographic distance significantly predicted community similarity in six of the nine regions. The three regions in which community



**Fig. 2** Linear regressions of median regional temperature and precipitation seasonality on mean regional absolute latitude. The proportion of variance explained ( $R^2$ ) and significance values ( $P$ ) are provided. Symbols correspond to regions in Fig. 1.

similarity was not significantly predicted by geographic distance were the three most southerly regions (Fig. 1); community similarity was also not significantly predicted by environmental distance in these three regions. Environmental distance was only a significant predictor of community similarity for the East African region; geographic distance was also a significant predictor in the East African region (Table III). Partial Mantel test results using the  $\beta_{\text{sim}}$  similarity index are included in Appendix S4.

### Predictors of Dispersal Limitation and Climate Variability Across Regions

Mean absolute regional latitude significantly predicted the dispersal limitation signal, i.e., the absolute value of the partial Mantel correlation ( $r$ ) between geographic distance and primate community similarity (linear regression:  $R^2=0.51$ ,  $df=7$ ,  $P=0.03$ ; Fig. 3), but not climatic effects on community similarity, i.e., the absolute value of the partial Mantel correlation ( $r$ ) between environmental distance and primate community similarity (linear regression:  $R^2=0.04$ ,  $df=7$ ,  $P=0.59$ ). This result is consistent with a significant latitudinal gradient in primate dispersal limitation across sub-Saharan Africa. In addition, comparable analyses conducted with the  $\beta_{\text{sim}}$  similarity index, which is independent of species richness, also produced a latitudinal gradient in the dispersal limitation signal (linear regression:  $R^2=0.63$ ,  $df=6$ ,  $P=0.01$ ) and did not find a

**Table III** Partial Mantel test results

ID	Name	Environmental distance		Geographic distance		Sample size <i>n</i>
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
1	Guinean	-0.04	0.44	<b>-0.40</b>	<b>0.03</b>	28
2	Nigerian	-0.08	0.30	<b>-0.19</b>	<b>0.01</b>	351
3	Ethiopian	-0.22	0.27	<b>-0.80</b>	<b>0.05</b>	10
4	Congolian	0.09	0.71	<b>-0.79</b>	<b>0.00</b>	171
5	Lake Tanganyikan	0.00	0.50	<b>-0.50</b>	<b>0.00</b>	66
6	East African	<b>-0.22</b>	<b>0.02</b>	<b>-0.44</b>	<b>0.00</b>	325
7	West Zambezan	-0.02	0.53	-0.16	0.31	15
8	East Zambezan	0.16	0.80	-0.43	0.10	45
9	South African	0.00	0.46	-0.02	0.39	153

Results of partial Mantel tests examining the relative strength of environmental filtering and dispersal limitation in each region based on the strength of the correlation ( $r$ ) between community similarity (Sørensen index) and environmental distance or geographic distance, respectively. Bold font indicates a significant predictor of primate community similarity ( $P \leq 0.05$ ). The sample size is the number of pairwise comparisons between sites for each region ( $n = N * (N - 1) / 2$  where  $N$  is the number of sites in each region). Gray shading indicates the stronger relative predictor for each region between environmental distance or geographic distance. Region numbers correspond to labels in Fig. 1. Study site: Africa; taxa: all primates.

significant relationship between latitude and environmental effects (linear regression:  $R^2=0.04$ ,  $df=6$ ,  $P=0.62$ ).

Regional area, or the spatial extent of each region, did not significantly predict dispersal limitation strength or environmental effects (linear regression: dispersal effects,  $R^2=0.11$ ,  $df=7$ ,  $P=0.39$ ; environmental effects,  $R^2=0.02$ ,  $df=7$ ,  $P=0.69$ ). In addition, mean regional latitude did not significantly predict regional area (linear regression: latitude,  $R^2<0.01$ ,  $df=7$ ,  $P=0.97$ ). This demonstrates that the latitudinal pattern was not driven by the spatial extent of the biogeographic regions.

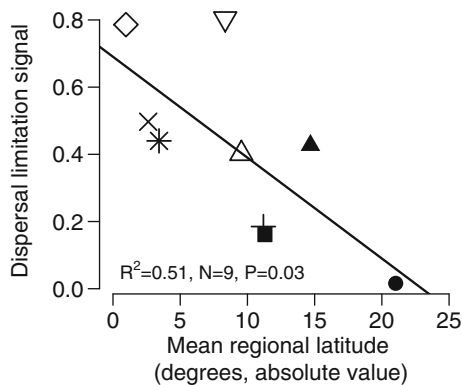
Neither regional species richness nor the difference in species richness between sites in a region significantly predicted dispersal limitation strength or environmental effects (species richness linear regression: dispersal effects,  $R^2=0.27$ ,  $df=7$ ,  $P=0.15$ ; environmental effects,  $R^2=0.01$ ,  $df=7$ ,  $P=0.79$ ; maximum site richness – minimum site richness linear regression: dispersal effects,  $R^2=0.13$ ,  $df=7$ ,  $P=0.34$ ; environmental effects,  $R^2<0.01$ ,  $df=7$ ,  $P=0.99$ ). This suggests that the gradient in dispersal limitation pattern was not driven by latitudinal variation in species richness.

## Discussion

### Dispersal-Ecological Specialization Hypothesis

In this study we found a significant latitudinal gradient in the signal of dispersal limitation in African primate assemblages. Our results extend support for the dispersal-ecological specialization hypothesis to nonhuman primates. Prior support has been found for other taxa and continental areas, including Neotropical birds (Salisbury *et al.* 2012), European beetles (Baselga *et al.* 2012), Mediterranean butterflies (Carnicer *et al.* 2013), and human cultures (Harcourt 2012).

We found that primate assemblages in regions closer to the equator were more strongly structured by dispersal limitation than those in regions at higher absolute



**Fig. 3** Linear regression of the primate dispersal limitation signal (the absolute value of the partial Mantel correlation ( $r$ ) between geographic distance and primate community similarity) on mean regional absolute latitude for each of the nine African biogeographic regions. The proportion of variance explained ( $R^2$ ) and significance values ( $P$ ) are provided. Symbols representing biogeographic regions correspond to the symbol legend in Fig. 1.

latitudes. This pattern was not an artifact of spatial scale because there was no relationship between the area of a biogeographic region and the effect sizes, i.e., the absolute value of the partial Mantel correlation ( $r$ ) between geographic distance and primate community similarity. Instead, variation in primate ecological specialization and gene flow may have produced this latitudinal gradient in dispersal limitation. Greater ecological specialization may result in reduced gene flow in tropical primates as individuals move shorter distances to track preferred resources and conditions. Several mammalian taxa, including primates, exhibit latitudinal gradients in home range size with smaller home ranges at lower latitudes (Bowman *et al.* 2002; Gompper and Gittleman 1991; Harcourt 1998; Lindstedt *et al.* 1986). Indeed the relationship between home range size and dispersal is so strong that home range size in addition to geographic range size and body size were the most important predictors of mammalian natal dispersal distances in a large-scale modeling analysis (Whitmee and Orme 2013). Further examination of the relationships between primate daily path length and latitude are needed. If shorter daily travel distance results in lower gene flow, this may further perpetuate ecological specialization based on the balance between the strength of selection for local resources and dispersal (Case and Taper 2000).

In Africa, many equatorial primate assemblages are located in rain forest habitat and consist of arboreal, forest-adapted species, such as forest guenons (genus: *Cercopithecus*) and colobus monkeys (genera: *Colobus*, *Ptilocolobus*, and *Procolobus*). The arboreal nature of these species may play an important role in dispersal limitation and consequently limit gene flow. In particular, extant guenon species diversity is thought to be connected to the changing extent and connectivity of African rain forests associated with climate change from the Miocene through the present (Grubb 1982; Kamilar *et al.* 2009; Tosi *et al.* 2005). Studies of primates and other arboreal animals in other regions have suggested that arboreality reduces the likelihood of these animals crossing open areas (Laurance 1990; Schwarzkopf and Rylands 1989). The absence of significant dispersal limitation in the three most southerly regions may be due to the reduced forest cover in these regions compared with tropical rain forests and thus fewer arboreal species. In addition, it has been shown that rivers function as barriers to dispersal for some primate species, particularly small-bodied and more specialized primates (Harcourt and Wood 2012). Lastly, the region with the highest dispersal limitation signal was the Ethiopian region in which the five sites straddled a mountain range, which suggests that mountains can also serve as barriers to dispersal for some primates. Indeed, mountains can function as islands in that some montane environments contain a higher proportion of endemic taxa (Rovero *et al.* 2009).

Geographic distance was a stronger predictor of primate community similarity than was environmental distance within each of the nine biogeographic regions, which suggests that dispersal limitation has been a stronger influence on primate communities than environmental filtering throughout biogeographic regions in sub-Saharan Africa. These results are consistent with similar analyses of African primate communities that have focused on single regions within Africa (Beaudrot and Marshall 2011; Beaudrot *et al.* 2013). An analysis of African primate assemblages at the continental scale, however, found that both spatial and environmental factors were significant predictors of primate community similarity (Kamilar 2009). Other analyses at the continental level

have found environmental effects of annual rainfall and forest cover area on African primate community species richness (Reed and Fleagle 1995). Taken together, these studies suggest that dispersal limitation is a strong influence on primate communities at the regional scale, but that environmental filtering also operates on primate communities at continental spatial scales.

East Africa was the only region in which primate community similarity was significantly predicted by environmental distance. A likely explanation for this pattern may be related to the fact that East Africa contains the highest environmental variation between sites in a region as measured in this study. A nonmutually exclusive alternative explanation may be due to the fact that East Africa was the only region for which a number of sites were excluded because they contained fewer than four primate species. The exclusion of some sites may have also contributed to the weaker delineation of this biogeographic region in the cluster analysis. A recent study quantified African biogeographic regions across several Classes and found a lack of consensus in parts of East Africa (Linder *et al.* 2012). In addition, whereas we partitioned the East African, West Zambesian, and East Zambesian regions, Linder *et al.* (2012) grouped them into a single region. Irrespective of the underlying cause of our result, the lack of consensus in cluster analyses of a number of other East African taxa (Linder *et al.* 2012) suggests that the biogeography of this region is highly complex.

Though we did not evaluate variation in primate ecological specialization across regions, several studies have previously demonstrated that specialization in primates is greater in the tropics and declines with absolute latitude. For example, catarrhine habitat breadth and diet breadth both increase with distance from the equator (Eeley and Foley 1999). In addition, Harcourt (2000) found that the diets of African primate genera with larger latitudinal extents contained a greater number of items.

### Rapoport Effect

Under the dispersal-ecological specialization hypothesis, species' dispersal limitation is expected to influence community composition more in the tropics than at higher absolute latitudes. Equatorial species are expected to be more dispersal limited because of their greater ecological specialization whereas more temperate species are expected to exhibit greater dispersal in response to variability in climatic conditions (Jocque *et al.* 2010).

Our findings are consistent with a latitudinal gradient in primate dispersal limitation and support the hypothesis that there are trade-offs in dispersal ability and ecological specialization, which in turn offers an explanation for the Rapoport effect, which is the pattern observed when geographic range sizes increase with distance from the equator (Rapoport 1982). African primates exhibit the Rapoport effect to varying extents (Eeley and Lawes 1999; Harcourt 2000). In addition to African primates exhibiting increases in geographic range size with increasing distance from the equator, geographic range size also positively correlates with increasing variability in climatic conditions, particularly rainfall (Cowlshaw and Hacker 1997; Harcourt 2000).

Some other previous explanations of the Rapoport effect have focused on the role of climate variability and thus share ideas in common with the dispersal-ecological specialization hypothesis. For example, Stevens (1989) argued that narrower climatic tolerance of tropical organisms drive smaller species ranges and thus climatic tolerances

drive the Rapoport effect. This argument follows from the classic treatise “Why mountain passes are higher in the tropics” (Janzen 1967). Neither Stevens (1989) nor Janzen (1967) made predictions about variation in ecological specialization across latitudes. Wiens and Donoghue (2004) further elaborated on the idea of climatic tolerances affecting dispersal. Their tropical niche conservatism hypothesis posits that phylogenetic niche conservatism, which in this case is the tendency for closely related species to exhibit similar climatic niches, has led to greater species richness in the tropics because the abiotic environment has limited species’ dispersal. However, current evidence for primates does not provide strong support for this hypothesis because closely related species often exhibit different climatic niches. A primate-wide analysis found low levels of phylogenetic signal (Blomberg’s  $K < 0.20$ ) for several climatic variables (Kamilar and Cooper 2013). Another study examining the evolution of Malagasy primate climatic niches also found a weak relationship between the evolutionary relatedness among species and their niche space (Kamilar and Muldoon 2010). The dispersal-ecological specialization hypothesis differs from these explanations in the following manner: Rather than climatic tolerances limiting distributions, it proposes that lower climatic variability allows for greater ecological specialization, e.g., on dietary resources, and relaxes selective pressure for high dispersal ability at lower absolute latitudes.

### Future Directions

Future studies may provide greater mechanistic insight into the dispersal-ecological specialization hypothesis in primates by focusing on individual species with distributions that span broad latitudinal swaths, e.g. *Chlorocebus aethiops*, *Papio ursinus*, *Papio cynocephalus*. In particular, comparative studies in multiple populations of a single species along a latitudinal gradient can directly test for latitudinal gradients in gene flow and dietary specialization. We note, however, that African nonhuman primates with large geographic ranges are not typically found in rain forest habitat. Therefore, the range of environmental conditions these species experience may not encompass the conditions experienced by rain forest-adapted taxa.

Because we tested for significant effects of environmental filtering and dispersal limitation using partial Mantel tests, which test for linear relationships, we did not quantify the contribution of nonlinear relationships within regions, but visual inspection of the data did not suggest nonlinear effects. Although the partial Mantel test has been used in ecology for more than two decades, some recent criticisms of this test (Guillot and Rousset 2013; Steinbauer *et al.* 2013; Tuomisto *et al.* 2012) highlight that additional examinations of the latitudinal gradient found in this study using other methods may be informative.

### Conclusions

A number of mechanisms in addition to dispersal limitation influence species distributions and community composition, for example interspecific interactions and historical factors (Fleagle *et al.* 1999; Kamilar and Beaudrot 2013; Reed and Bidner 2004). It is therefore noteworthy that latitude explained more than half of the variation in African

primate dispersal limitation in this study. Strong dispersal limitation in equatorial African primate assemblages and a significant decline in dispersal limitation with increasing latitude is consistent with the hypothesis that climate variability drives trade-offs between dispersal ability and ecological specialization. Previous meta-analyses of the species attributes associated with dispersal limitation have largely focused on temperate studies and have included few mammalian taxa (Cottenie 2005; Soininen *et al.* 2007). This study highlights that meta-analyses to date may have failed to detect important differences between temperate and tropical faunal community assembly and demonstrates how studies of primate assemblages can provide insight into general principles of ecology and biogeography.

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