The Influences of Species Richness and Climate on the Phylogenetic Structure of African Haplorhine and Strepsirrhine Primate Communities

Jason M. Kamilar · Lydia Beaudrot · Kaye E. Reed

Abstract Many factors contribute to the structure of primate communities, including historical processes, interspecific competition, and climate. Here, we quantify the phylogenetic structure of individual primate communities to evaluate these factors relative to a null model. Then, we examine the effects of species richness and local climate on variation in community phylogenetic structure. We analyze 71 haplorhine and 29 strepsirrhine communities in Africa and quantify their net relatedness (NRI) and nearest taxon (NTI) indices. Significantly low, i.e., phylogenetically even, NRI and NTI values are indicative of interspecific competition in the past, resulting in closely related species not being found in the same community. In contrast, significantly high, i.e., phylogenetically clustered, NRI and NTI values suggest that closely related species have similar ecological requirements, resulting in closely related species occupying the same community. In a second set of analyses, we used simultaneous autoregressive models to examine if species richness, rainfall, and temperature predict variation in community phylogenetic structure. Most individual communities exhibited phylogenetically random species assemblages. However, significantly structured haplorhine

J. M. Kamilar (✉)
School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona 85287, USA
e-mail: jkamilar@midwestern.edu

J. M. Kamilar
Department of Anatomy, Arizona College of Osteopathic Medicine, Midwestern University, Glendale, Arizona 85308, USA

L. Beaudrot
Graduate Group in Ecology and Department of Anthropology, University of California, One Shields Avenue, Davis, California 95616, USA

K. E. Reed
School of Human Evolution and Social Change and Institute of Human Origins, Arizona State University, Tempe, Arizona 85287, USA

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communities were even whereas strepsirrhine communities were clustered. Species richness significantly predicted variation in haplorhine phylogenetic structure, whereas abiotic factors significantly predicted variation in strepsirrhine phylogenetic structure. We suggest that past interspecific competition and habitat filtering have affected a relatively small proportion of African primate communities, but that past interspecific competition has more strongly influenced haplorhine communities whereas environmental conditions have more strongly influenced strepsirrhine communities. Our study illustrates the utility of phylogenetic metrics and spatially explicit models for understanding primate communities.

Introduction

Understanding the factors driving the distribution and co-occurrence of species is a fundamental question in ecology and evolution. The study of community-level phylogenetic patterns has become a major subfield of ecology as a means for understanding how communities of organisms are assembled (Webb *et al.* 2002). Many of the community phylogenetic analyses to date (Cardillo 2011; Cardillo *et al.* 2008; Cooper *et al.* 2008b) have focused on testing whether individual communities comprise species that are more or less related than expected under a null model. In particular, community phylogenetic patterns may exhibit 1) significant phylogenetic evenness, i.e., overdispersion, which has been argued to be the result of past interspecific competition resulting in the competitive exclusion of closely related species and, therefore, communities that contain species with few close relatives; or 2) significant phylogenetic clustering, which has been argued to be the result of environmental and habitat conditions filtering for specific traits that are well adapted to the local environment (hereafter "habitat filtering") and thus resulting in communities of organisms that are more closely related than would be expected based on chance alone.

Even when an individual community does not contain a significant level of phylogenetic structure, hylogenetic structure metrics can contain important biological information about the community that can be subsequently connected to local ecological factors. For example, the phylogenetic structure of Andean hummingbird communities varied in a predictable fashion across environmental gradients (Graham *et al.* 2009). In particular, phylogenetically clustered communities were found in cool and moist high elevation habitats or seasonally dry and warm environments. In contrast, these communities were more likely to be phylogenetically even in warm and wet lowlands. In many ways, this approach is analogous to the concept of ecological convergence, in which similar selective pressures in spatially isolated environments independently produce similar adaptations. Of course, the causal mechanisms influencing ecological communities are notoriously difficult to discern (Connor and Simberloff 1979). Yet multiple and independent studies finding correlations between biological traits (including community structure) and various aspects of the abiotic and biotic environment lend support to the idea that causal relationships exist (Martins 2000).

Within the field of primate community ecology, early research focused on the ecological niche as a fundamental unit of structure for primate communities (Bourliere 1985; Ganzhorn 1989). Further developments highlighted the role of broad-scale environmental factors, including rainfall and plant productivity, influencing primate species richness (Kay *et al.* 1997; Reed and Fleagle 1995). Recent studies have called attention to the importance of historical processes in primate community assembly, such as the likelihood that individuals of a particular primate species can reach and successfully colonize a site (Beaudrot and Marshall 2011; Gavilanez and Stevens 2013; Kamilar 2009; Muldoon and Goodman 2010). Other studies have used a phylogenetic approach to examine the potential influences of past interspecific competition and current environmental conditions for shaping community structure (Cardillo *et al.* 2008; Kamilar and Guidi 2010). For primates, a previous analysis at the global level found that most communities do not exhibit significant phylogenetic patterning, but instead are composed of species that are randomly sorted from the primate phylogeny (Kamilar and Guidi 2010). Yet, Malagasy primate communities were significantly more phylogenetically even compared to other regions. The unique biogeographic history of Madagascar may play an important role in this pattern (Wilmé *et al.* 2006). Nonetheless, although it has been established that the majority of primate communities are phylogenetically random, what remains an open question is the extent to which the phylogenetic structure of primate communities has converged in geographically separate, but environmentally similar habitats.

A recent study of convergence in mammalian communities suggested that small-bodied arboreal secondary consumers exhibit the highest levels of convergence compared to mammals occupying other niches (Louys *et al.* 2011). This study highlights the importance of examining ecological convergence in the phylogenetic structure of primates that fit these characteristics, particularly strepsirrhines. Existing studies of convergence in primate ecology have focused on the extent to which social structure and behavioral ecology exhibit convergence across species and biogeographic regions (DiFiore and Rendall 1994; Kamilar and Cooper 2013; Kamilar and Muldoon 2010; Kappeler and Heymann 1996; Kappeler and van Schaik 2002; Ossi and Kamilar 2006; van Schaik and Kappeler 1996). Within primate community ecology, substantial differences in food sources across regions have been argued to be the reason for little convergence in primate communities (Terborgh and van Schaik 1987). Furthermore, primate communities are more ecologically similar within a region compared to between regions (Fleagle and Reed 1996), but overlap in niche space suggests at least some ecological convergence despite a clear role of phylogenetic history influencing community composition (Fleagle *et al.* 1999).

Previous studies have focused on the phylogenetic structure of primate communities at the order level (Cooper *et al.* 2008b; Kamilar and Guidi 2010). Yet, there is important biological variation within the order, especially at the suborder level. From an ecological perspective, haplorhine primates are generally large, diurnal animals that feed on fruit and leaves, whereas strepsirrhine primates are small, nocturnal taxa that feed on fruit, insects, and exudates (Fleagle 2013). This dichotomy is especially true for primates in African and Asia. In addition, there are significant macroecological and evolutionary patterns that differ between the two groups. Compared to African strepsirrhines, haplorhines occupy a wider range of ecological niches (as defined by body mass variation, specialized folivory, and degree of terrestriality) and are often

found living sympatrically with several other haplorhine species (Fleagle *et al.* 1999). The substantial niche differences between suborders, i.e., haplorhini vs. strepsirrhini, may drive differences in the effects of interspecific competition and habitat filtering on community structure in these two suborders. Therefore, examining the phylogenetic structure of primate communities at the suborder level may yield important insights into the ecology and evolution of primates.

Africa is one of only two continents where both haplorhine and strepsirrhine primates are found sympatrically. In addition, African primates live in a wide variety of environments, which make an excellent system to examine the influences of environmental factors on community structure. Therefore, in this article we examine the phylogenetic structure of African haplorhine and strepsirrhine communities. In the first of two sets of analyses, we quantify the phylogenetic structure of individual African haplorhine and strepsirrhine communities. Communities may comprise relatively distantly related species, suggesting that past interspecific competition has resulted in the local extinction of closely related taxa. Alternatively, communities may contain closely related species assemblages, indicating that biological traits shared among these taxa may be connected to local environmental conditions. In a second set of analyses, we examine if species richness and climatic factors predict variation in the phylogenetic structure of communities across continental Africa at the suborder level. We predict that species richness will have a stronger effect on haplorhine communities because there is more variation in haplorhine species richness across sites and haplorhine species richness within sites is higher on average than strepsirrhine species richness. Therefore, we predict that increasing haplorhine species richness should be related to increasing phylogenetic distance between species in communities. We also predict that the phylogenetic structure of strepsirrhine communities will be more influenced by climatic factors because small mammals may be more sensitive to environmental variation owing to the increased cost of thermoregulation and seasonal shifts in food availability (Boyce 1979; Kamilar *et al.* 2012; Terborgh and van Schaik 1987; Watt *et al.* 2010).

Methods

Data Collection

We compiled presence-absence data for 59 African primate taxa (45 haplorhine species and 14 strepsirrhine species deriving from localities having four or more primates) from 72 study sites (see Electronic Supplementary Material [ESM]). From the 72 sites, we quantified the phylogenic structure of 71 haplorhine communities and 29 strepsirrhine communities using two metrics. The only site that contained four or more strepsirrhine species but did not also contain four or more haplorhine species was Kizigo Game Reserve in Tanzania. For each extant locality, we obtained data on geographic location and environmental conditions. Localities were recorded with centralized geospatial coordinates from the center of the site's latitude and longitude.

We obtained high-resolution climate data from the WorldClim database based on the latitude and longitude coordinates (Hijmans *et al.* 2005). This climate database has been extensively used in community ecology and biogeography

research as evidenced by its extensive citation record (Cooper *et al.* 2008a; Beaudrot and Marshall 2011; Graham *et al.* 2012; Kamilar and Marshack 2012; Kamilar and Muldoon 2010). The Worldclim database contains 19 climate variables representing temperature and rainfall variation, as well as altitude data. The climate variables are based on >50 yr of data from worldwide weather stations. In addition to quantifying the abiotic environment, these variables serve as proxies of habitat structure (Murphy and Lugo 1986; Whittaker 1975). Many of the 19 climate variables are highly correlated with each other (Beaudrot and Marshall 2011). Therefore, we chose to focus on six variables that represent average and seasonal variation in rainfall and temperature: 1) annual mean temperature, 2) temperature seasonality (monthly standard deviation * 100), 3) minimum temperature of coldest month, 4) mean annual precipitation, 5) precipitation of driest month, and 6) precipitation seasonality (monthly coefficient of variation). These and similar variables have been commonly used in prior studies of primate community ecology and macroecology (Blair *et al.* 2013; Kamilar and Bradley 2011; Kamilar *et al.* 2012; Lehman 2000; van Schaik *et al.* 2005).

Data Analysis

We quantified the phylogenetic structure of each community in the haplorhine and strepsirrhine datasets using two measures, the net relatedness index (NRI) and the nearest taxon index (NTI). Both metrics can be considered a "standardized effect size" of phylogenetic structure because the values of both metrics are relative to all sites considered. The NRI quantifies the mean phylogenetic distance among all taxa in a community relative to randomized sample of null communities based on all possible taxa found in the species pool, i.e., all possible species found in all communities in each dataset.

$$\mathrm{NRI}_{\mathrm{sample}} = -1^{*}\left(\mathrm{MPD}_{\mathrm{sample}} - \mathrm{MPD}_{\mathrm{rnd\ comm}}\right) / \left(\mathrm{sdMPD}_{\mathrm{rnd\ comm}}\right)$$

where $\mathrm{MPD}_{\mathrm{sample}}$ is the observed mean phylogenetic distance between all species pairs in a given community, $\mathrm{MPD}_{\mathrm{rnd\ comm}}$ is the mean phylogenetic distance between all species pairs in the randomized communities, and $\mathrm{sdMPD}_{\mathrm{rnd\ comm}}$ is the standard deviation of the phylogenetic distance in the randomized communities. Thus, NRI accounts for the evolutionary diversity of communities at multiple taxonomic/ phylogenetic levels.

The NTI is calculated in a similar fashion as NRI, except that it quantifies the phylogenetic distance among the most closely related taxa in a community, relative to a randomized sample of null communities constructed from the total species pool.

$$\mathrm{NTI}_{\mathrm{sample}} = -1^{*}\left(\mathrm{MNND}_{\mathrm{sample}} - \mathrm{MNND}_{\mathrm{rnd\ comm}}\right) / \left(\mathrm{sdMNND}_{\mathrm{rnd\ comm}}\right)$$

where $\mathrm{MNND}_{\mathrm{sample}}$ is the observed mean nearest phylogenetic neighbor distance in a given community, $\mathrm{MNND}_{\mathrm{rnd\ comm}}$ is the mean nearest phylogenetic neighbor distance in the randomized communities, and $\mathrm{sdMNND}_{\mathrm{rnd\ comm}}$ is the standard deviation of the mean nearest phylogenetic neighbor distance in the randomized communities. Thus the NTI measures more recent temporal aspects of community structure by quantifying only the phylogenetic distance among the most closely related species in a community.

Low NRI and NTI values, i.e., phylogenetic evenness, may indicate that interspecific competition in the past has resulted in closely related species not being found in the same community because of competitive exclusion. In contrast, high NRI and NTI values, i.e., phylogenetic clustering, are often thought to be the result of habitat filtering. This is the case because closely related species tend to have similar ecological requirements and therefore, are found in the same habitat and thus community. Communities may also exhibit phylogenetically random species compositions, yielding NRI and NTI scores that are not significantly different from zero (Webb *et al.* 2008) (Fig. 1). It is possible for individual primate communities to exhibit a phylogenetic structure no different than random, though among-community variation in phylogenetic structure could still be significantly predicted by species richness and/or climatic factors. This is because the phylogenetic structure metrics (NRI and NTI) are informative, even if they are not statistically different from zero. For example, a community with a NRI value of 1.5 comprises more closely related species than a community with a NRI a value of 0.5, even though both communities may not exhibit a high enough NRI to be considered significantly greater than zero.

The NRI and NTI analyses were conducted with PHYLOCOM (Webb *et al.* 2008). We used 9999 randomizations to calculate statistical significance. In addition, we used the independent swap null model, as this has important advantages over other null models. Specially, this model is not influenced by phylogenetic signal in species prevalence, i.e., closely related species are found in communities at similar frequencies (Kembel 2009). We used a primate consensus tree presented in the 10K Trees Project Version 3 (Arnold *et al.* 2010). In addition, we followed the Genbank taxonomy associated with that phylogeny for consistency. Previous macro-level studies of primate community ecology showed that variation in taxonomic schemes has little effect on analytical results (Kamilar 2009; Kamilar and Guidi 2010). To examine the sensitivity of our results to phylogeny, we conducted a second set of analyses using another recently published primate tree (Springer *et al.* 2012).

We used simultaneous autoregressive models (SAR) (Dormann *et al.* 2007) to examine the importance of species richness and climate variables for predicting
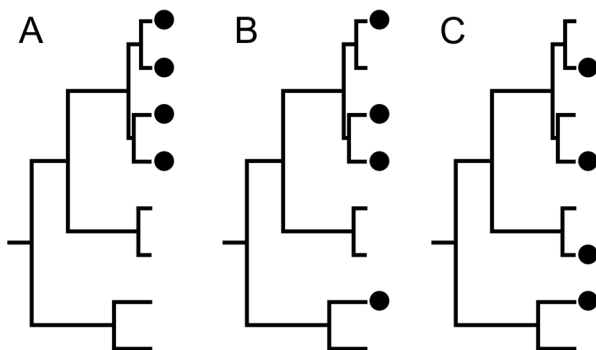

Fig. 1 Illustrations of community phylogenetic structure patterns (Webb *et al.* 2002). **(A)** phylogenetic clustering. **(B)** Phylogenetic randomness. **(C)** Phylogenetic evenness, i.e., overdispersed. The tips of the tree represent all taxa in the species pool, i.e., all possible taxa that can exist in a community. The circles at the end of the tips represent the species present in a hypothetical community. Each community in these illustrations contains four species.

community phylogenetic metrics, while accounting for spatial autocorrelation in the error structure of the model. The SAR is a generalized linear model that uses the latitude and longitude of each site as the basis for a matrix that modifies the error structure of the model. This technique removes the confounding effects of space, thereby reducing the possibility of spurious results. We conducted separate analyses for each metric (NRI and NTI) and for each of the haplorhine and strepsirrhine datasets (four analyses in total). We used Spatial Analysis in Macroecology (Rangel *et al.* 2010) to conduct all SAR analyses.

All tests were two-tailed and we considered $P \leq 0.05$ as statistically significant.

Results

Using the 10K Trees phylogeny Arnold et al. (2010), we found that one of the 71 haplorhine communities (Congo Basin site in the Democratic Republic of Congo [DRC]) were significantly phylogenetically even, i.e., phylogenetically overdispersed based on the NRI metric (Table I and Fig. 2; ESM); none of the strepsirrhine communities exhibited this pattern. In contrast, no haplorhine communities were significantly phylogenetically clustered, whereas two of 29 strepsirrhine communities (Kizigo and Selous game reserves in Tanzania) displayed this type of community structure. We found similar results when using NTI to quantify the phylogenetic structure of communities. For haplorhines, two of the 71 communities were significantly even (Massif du Ziama Biosphere Reserve in Guinea and Salongo National Park in the DRC) (Fig. 2), and again, significant phylogenetic evenness was not exhibited by a single strepsirrhine community. In contrast, only one haplorhine community was significantly clustered (Kibale National Park in Uganda), as opposed to two strepsirrhine communities (Kizigo and Selous game reserves in Tanzania). Using the Springer *et al.* (2012) phylogeny produced similar results, but the Massif du Ziama haplorhine community was no longer statistically significant ($P = 0.11$) and the Ruvubu National Park strepsirrhine community was phylogenetically clustered using NTI at a statistically significant level ($P = 0.02$; Table I).

Using the Arnold *et al.* (2010) phylogeny, variation in the phylogenetic structure of haplorhine communities (using both NTI and NRI) was significantly predicted by species richness (Tables II and III). In particular, as species richness increased, the evolutionary relatedness of taxa within communities declined, i.e., communities became more phylogenetically even. This result also suggests that small haplorhine communities tend to contain closely related taxa. In contrast, species richness did not have an important effect on the phylogenetic structure of strepsirrhine communities. Strepsirrhine communities were more influenced by climatic factors. Specifically, temperature seasonality and precipitation seasonality were significant predictors of both NRI and NTI values for strepsirrhine communities. As temperature seasonality increased, strepsirrhine communities became more phylogenetically even, which is consistent with the interpretation of interspecific competition dominating community assembly. In contrast, as precipitation seasonality increased, strepsirrhine communities become more phylogenetically clustered, i.e., they exhibited higher NTI and NRI values, which is consistent with the interpretation of habitat filtering as the influential assembly process. Most of

Table I The phylogenetic structure of haplorhine and strepsirrhine communities in Africa

	No. of communities	No. of low NRI	% Low NRI	No. of high NRI	% High NRI	No. of low NTI	% Low NTI	No. of high NTI	% High NTI
Dataset using Arnold et al. 2010 phylogeny									
Haplorhines	71	1	1.4	0	0.0	2	2.8	1	1.4
Strepsirrhines	29	0	0.0	2	6.9	0	0.0	2	6.9
Dataset using Springer et al. 2012 phylogeny									
Haplorhines	71	1	1.4	0	0.0	1	1.4	1	1.4
Strepsirrhines	29	0	0.0	3	10.3	0	0.0	3	10.3

Only communities with at least four species were included in the analyses. NRI = Net relatedness index; NTI = Nearest taxon index.

No. of low are the number of communities exhibiting significantly low values; No. of high are the number of communities exhibiting significantly high values.

Low values indicate that communities contain relatively distantly related species, whereas high values indicate that communities contain relatively closely related species.
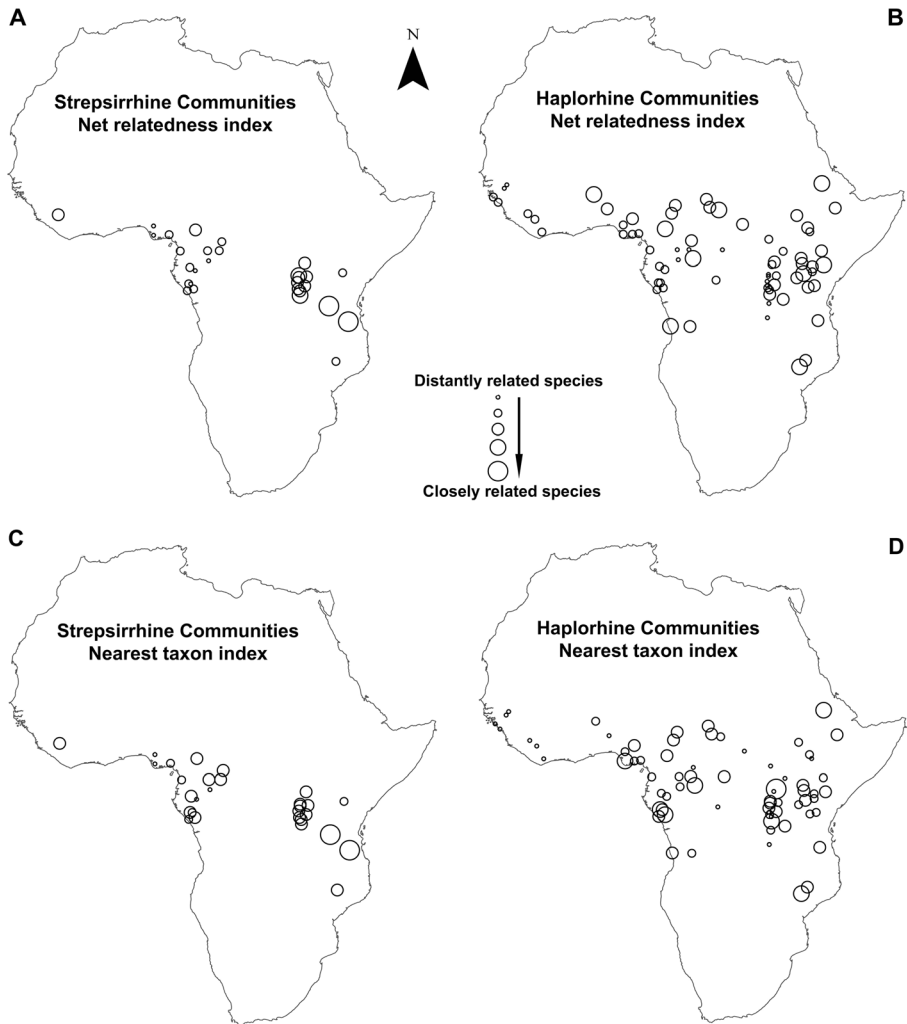
Fig. 2 The phylogenetic structure of **(A)** strepsirrhine and **(B)** haplorhine communities in Africa as measured by the net relatedness index (NRI). The phylogenetic structure of **(C)** strepsirrhine and **(D)** haplorhine communities in Africa as measured by the nearest taxon index (NTI). Small circles indicate negative NRI/NTI values, i.e., communities that tend toward phylogenetic evenness, and large circles indicate positive NRI/NTI values, i.e., communities that tend toward phylogenetic clustering. Communities with NRI/NTI values around zero are illustrated by medium sized circles.

the models produced similar results when using the Springer *et al.* (2012) (Tables IV and V). For haplorhine communities, both NRI and NTI were best predicted by species richness. For strepsirrhine communities, NRI was best predicted by temperature and precipitation seasonality. These variables were not statistically significant in the model predicting NTI variation across strepsirrhine communities, though precipitation seasonality exhibited a P value of 0.058. Interestingly, the significance level of the overall model was nearly identical to the analogous analysis using the Arnold *et al.* (2010) phylogeny, $P = 0.048$ and $P = 0.049$, respectively.

Table II Results of simultaneous autoregressive models predicting the NTI of haplorhine and strepsirrhine communities in Africa from species richness and climate data

	Haplorhines		Strepsirrhines	
	Std. coeff.	P value	Std. coeff.	P value
Species richness	**−0.305**	**0.023**	0.147	0.384
Mean annual mean temp	−0.403	0.316	0.757	0.307
Temperature seasonality	−0.011	0.965	**−0.956**	**0.019**
Minimum temperature during coldest month	0.303	0.393	−0.832	0.217
Mean annual precipitation	−0.205	0.201	−0.160	0.441
Precipitation in driest month	0.446	0.109	0.154	0.645
Precipitation seasonality	0.567	0.060	**0.952**	**0.043**
Total model results	$F = 1.010$; $P = 0.433$; $N = 71$		$F = 2.506$; $P = 0.049$; $N = 29$	

Based on the Arnold *et al.* 2010 primate phylogeny.

Statistically significant predictors are in bold. NTI = nearest taxon index.

Discussion

A large proportion of individual haplorhine and strepsirrhine communities lacked a significant amount of phylogenetic structure, i.e., the composition of species did not differ from a phylogenetically random assemblage. However, the communities that were significantly structured exhibited a phylogenetically even pattern for haplorhines and a clustered pattern for strepsirrhines. In addition, our results from the simultaneous autoregressive models demonstrate the significant influence of species richness and local climate (and therefore, habitat) on among-site variation in the phylogenetic structure of haplorhine and strepsirrhine communities, respectively. This illustrates the distinction between testing whether an individual

Table III Results of simultaneous autoregressive models predicting the NRI of haplorhine and strepsirrhine communities in Africa from species richness and climate data

	Haplorhines		Strepsirrhines	
	Std. coeff.	P value	Std. coeff.	P value
Species richness	**−0.520**	**<0.001**	0.041	0.770
Mean annual mean temp	−0.004	0.990	−0.224	0.711
Temperature seasonality	−0.296	0.168	**−0.938**	**0.006**
Minimum temperature during coldest month	0.039	0.900	0.162	0.767
Mean annual precipitation	−0.076	0.591	−0.076	0.657
Precipitation in driest month	0.137	0.575	0.046	0.867
Precipitation seasonality	0.375	0.156	**0.853**	**0.029**
Total model results	$F = 5.293$; $P < 0.001$; $N = 71$		$F = 4.373$; $P = 0.004$; $N = 29$	

Based on the Arnold *et al.* 2010 primate phylogeny.

Statistically significant predictors are in bold. NRI = net relatedness index.

Table IV Results of simultaneous autoregressive models predicting the NTI of haplorhine and strepsirrhine communities in Africa from species richness and climate data

	Haplorhines		Strepsirrhines	
	Std. coeff.	P value	Std. coeff.	P value
Species richness	**−0.314**	**0.024**	−0.198	0.186
Mean annual mean temp	−0.24	0.564	−0.493	0.444
Temperature seasonality	−0.093	0.711	−0.504	0.139
Minimum temperature during coldest month	0.135	0.714	0.418	0.472
Mean annual precipitation	−0.197	0.237	−0.103	0.569
Precipitation in driest month	0.434	0.133	0.031	0.915
Precipitation seasonality	0.586	0.061	0.776	0.058
Total model results	$F = 1.393; P = 0.224; N = 71$		$F = 2.510; P = 0.048; N = 29$	

Based on the Springer *et al.* 2012 primate phylogeny.

Statistically significant predictors are in bold. NTI = nearest taxon index.

community is phylogenetically structured versus explaining *variation* in phylogenetic structure across sites. As haplorhine communities increase in species richness, the average phylogenetic distance among species increases, as does the distance among closely related species. This pattern may be the result of past interspecific competition. For strepsirrhine communities, increasing temperature seasonality results in more phylogenetically diverse communities. In contrast, as rainfall seasonality increases, strepsirrhine communities comprise more closely related species. These results suggest that climatic factors are important for understanding African strepsirrhine distributions and co-occurrence patterns.

Table V Results of simultaneous autoregressive models predicting the NRI of haplorhine and strepsirrhine communities in Africa from species richness and climate data

	Haplorhines		Strepsirrhines	
	Std. coeff.	P value	Std. coeff.	P value
Species richness	**−0.512**	**<0.001**	0.012	0.930
Mean annual mean temp	0.093	0.787	-0.277	0.645
Temperature seasonality	−0.361	0.085	**-0.770**	**0.021**
Minimum temperature during coldest month	−0.077	0.801	0.182	0.738
Mean annual precipitation	−0.087	0.528	-0.036	0.832
Precipitation in driest month	0.131	0.581	-0.053	0.845
Precipitation seasonality	0.361	0.161	**0.754**	**0.050**
Total model results	$F = 5.573; P < 0.001; N = 71$		$F = 4.152; P = 0.005; N = 29$	

Based on the Springer *et al.* 2012 primate phylogeny.Statistically significant predictors are in bold.

NRI = Net relatedness index

Why Do Most Individual Communities Exhibit a Random Phylogenetic Structure?

Our finding that most individual communities do not exhibit a significant amount of phylogenetic structure is similar to previous results found at the Order level (Kamilar and Guidi 2010). This pattern may indicate a relatively weak effect of interspecific competition within suborders at most sites. Instead, competition with nonprimate species may be more important for structuring communities than competition between primate species. One line of evidence that supports this explanation is the presence of significant phylogenetic structure in Malagasy primate communities where primates dominate the terrestrial mammalian fauna (Beaudrot and Marshall 2011; Kamilar and Beaudrot 2013). In fact, Malagasy communities were more often phylogenetically even compared to primate communities in other regions (Kamilar and Guidi 2010), which suggests that past competition between closely related species may have resulted in competitive exclusion. This was further supported by a more recent finding that showed a similar pattern while including subfossil lemur species when quantifying the phylogenetic structure of modern Malagasy primate communities (Razafindratsima *et al.* 2012). Competition among Malagasy primates may be greater than competition between primate species in other regions, such as mainland Africa, where primates are a smaller proportion of the mammalian fauna.

The majority of research addressing primate community ecology to date has focused on primates alone, without quantitative analyses considering the potential influences of other mammals on primate communities. Yet studies that have incorporated other taxonomic groups have reported striking results that suggest consideration of interactions between primates and other taxa is warranted. For example, a detailed study from Gabon of 32 fruit-eating vertebrate species including six primate species and the fruits they consume highlighted the dietary overlap and thus the potential for competition between monkeys and hornbills (Gautier-Hion *et al.* 1985). Other studies in Asia have found evidence that dietary overlap and interspecific competition may be highest between primate and non-primate vertebrates (Beaudrot *et al.* 2013; Marshall *et al.* 2009). In the Neotropics, species from the order Pilosa (sloths) have been hypothesized to compete with folivorous New World monkeys (Reed and Bidner 2004). Thus, unmeasured competition between primate species and other taxa may have influenced the results of this present study. Though, it is unclear whether future community ecology studies using a phylogenetic approach would benefit from including a broader, i.e., nonprimate vertebrates, taxonomic sample because these methods assume that closely related species have similar biological traits and this similarity decreases with increasing phylogenetic distance. Testing this assumption could be an important aspect of future work (Mayfield and Levine 2010).

Another possible explanation for the low levels of significant phylogenetic structure is that consideration of additional data, such as species traits, is needed to draw meaningful conclusions about the underlying processes affecting phylogenetic structure and community composition (Kraft *et al.* 2008; Swenson 2013). The phylogenetic evenness/clustered framework assumes that closely related species exhibit more similar traits (and resulting niches) and thus compete more with each other than with distantly related species. However, phylogenetic signal varies widely for many primate traits that may be relevant for interspecific competition

(Kamilar and Cooper 2013). Therefore, low levels of phylogenetic structure may be due to relatively weak phylogenetic signal in traits that are related to interspecific competition and/or habitat filtering.

Predicting the Phylogenetic Structure of Haplorhine Communities

Most haplorhine communities exhibited a phylogenetic structure no different from random, but the communities that were significantly structured were phylogenetically even. A traditional interpretation of phylogenetic evenness would be that the structured communities are the product of past interspecific competition, which has resulted in modern communities containing distantly related species (Webb *et al.* 2002). The importance of interspecific competition for structuring haplorhine communities can also be inferred from the positive association between species richness and increasing NRI and NTI values. As the species richness at a site increases, the phylogenetic distance among species and among closely related taxa also increases. In addition, the increased phylogenetic distances among taxa in large communities may be related to increases in the number and diversity of niches in habitats with high species richness. Haplorhine primates are found in a wide array of habitats in Africa, ranging from relatively dry and xeric environments to lush rain forests. Although climatic variables themselves did not significantly predict the phylogenetic structure of haplorhine communities (though precipitation seasonality exhibited the highest estimate with an associated 0.06 P value for the NTI model), there is likely a general relationship between species richness and plant productivity (Kay *et al.* 1997; Reed and Fleagle 1995). Forest and especially rain forest habitats contain higher plant diversity, which provides the opportunity for a wider range of ecological niches compared to woodland and savanna locales with lower plant diversity (Pianka 1966; Wright 2002). Phylogenetically diverse communities comprising many species almost certainly fill more niches than small communities. For example, colobine monkeys and great apes are more often found in species rich communities and are usually absent in small ones. These two primate clades are ecologically distinct (and therefore, occupy distinct niches) compared to other haplorhines, especially with regard to their diet, body mass, and locomotor behavior (Fleagle 2013).

Predicting the Phylogenetic Structure of Strepsirrhine Communities

Unlike the haplorhine communities, the phylogenetic structure of strepsirrhine communities was not related to variation in species richness. This is likely due to the low variation in species richness and lower absolute levels of species richness compared to African haplorhine communities. Also unlike the haplorhine communities, strepsirrhine phylogenetic structure was significantly related to temperature and rainfall seasonality, and thus habitat filtering. Increases in rainfall seasonality were associated with communities with closely related species, which tend to be adapted to more environments with longer dry seasons. The taxa responsible for this strepsirrhine pattern are likely to be members of the Galaginae subfamily, which includes several species that known to live sympatrically, particularly in drier habitats. In addition, galagos are likely to drive the African strepsirrhine pattern because they account for nearly all the diversity of this clade.

In theory, we could directly test this by conducting additional analyses only using galago species, though this is not feasible because it would reduce the sample size to an insufficient level for statistical analyses.

Seasonally dry habitats present a challenge to many species in terms of seasonal limitations in food availability and diversity (Hemingway and Bynum 2005). Several Galaginae species, e.g., *Galago moholi*, *Euoticus elegantalus*, *Otolemur crassicaudatus*, overcome this challenge by using tree gum as an important dietary resource (Nash 1986; Nekaris and Bearder 2007). The presence of a more reliable food source in relatively unproductive habitats may allow multiple galago species to coexist in the same community. Therefore, rain seasonality may serve as an environmental filter for strepsirrhines, resulting in an increased likelihood for the coexistence of species with specialized dietary adaptations.

The effects of temperature seasonality on strepsirrhine communities were opposite to the effects of precipitation seasonality. Whereas communities of closely related strepsirrhines inhabited sites with high precipitation seasonality, closely related strepsirrhines were found in sites with low temperature seasonality. In the latter case, most strepsirrhine communities in our dataset contain some of the smallest galago species, e.g., female *Galagoides demidovii* weigh 60 g and are found in 25 communities and *Galagoides thomasi* weigh 130 g and are found in 19 communities (Smith and Jungers 1997). Therefore, the effects of temperature seasonality likely represent a different form of environmental filtering. In this case, sites with higher temperature stability may enable the long-term coexistence of small galago species that are sensitive to temperature variation. The connection between temperature and strepsirrhine community structure may be based on the increased metabolic demands for small mammals in locations with seasonally cold temperatures (Bergmann 1847; Watt *et al.* 2010). Conversely, sites with high temperature seasonality were associated with strepsirrhine communities that contained relatively distantly related species. This may be the result of past interspecific competition due to seasonal shifts in insect abundance that has resulted in competitive exclusion. Many African strepsirrhines rely on animal matter as a critical source of protein (Nekaris and Bearder 2007). If substantial reductions in insect abundance occur on a seasonal basis (Frith and Frith 1985; Kai and Corlett 2002), then closely related species with similar insect-based dietary requirements may not be able to coexist.

In conclusion, we found important differences in the phylogenetic structure of African haplorhine and strepsirrhine communities, with the former more commonly exhibiting phylogenetically even communities and the latter more frequently displaying phylogenetically clustered communities. In addition, we discovered that among-site variation in the phylogenetic structure of haplorhine communities was related to species richness. In contrast, among-site variation in the structure of strepsirrhine communities was most strongly predicted by abiotic factors. These findings are likely related to the stark differences in the biological traits exhibited by members of these clades and how this variation translates to community level patterns.

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