

ORIGINAL  
ARTICLE

# The phylogenetic structure of primate communities: variation within and across continents

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## ABSTRACT

**Aim** Our goals are: (1) to examine the relative degree of phylogenetic overdispersion or clustering of species in communities relative to the entire species pool, (2) to test for across-continent differences in community phylogenetic structure, and (3) to examine the relationship between species richness and community phylogenetic structure.

**Location** Africa, Madagascar, Asia, and the Neotropics.

**Methods** We collected species composition and phylogenetic data for over 100 primate communities. For each community, we calculated two measures of phylogenetic structure: (1) the net relatedness index (NRI), which provides a measure of the mean pairwise phylogenetic distance among all species in the community; and (2) the nearest taxon index (NTI), which measures the relative phylogenetic distance among the closest related species in a community. Both measures are relative to the phylogeny of the species in the entire species pool. The PHYLOCOM package uses a randomization procedure to test whether the NRI and NTI values are higher or lower than expected by chance alone. In addition, we used a Kruskal–Wallis test to examine differences in NRI and NTI across continents, and linear regressions to examine the relationship between species richness and NRI/NTI.

**Results** We found that the majority of individual primate communities in Africa, Asia and the Neotropics consist of member species that are neither more nor less closely related than expected by chance alone. Yet 37% of Malagasy communities contain species that are more distantly related to each other compared with random species assemblages. Also, we found that the average degree of relatedness among species in communities differed significantly across continents, with African and Malagasy communities consisting of more distantly related taxa compared with communities in Asia and the Neotropics. Finally, we found a significant negative relationship between species richness and phylogenetic distance among species in African, Asian and Malagasy communities. The average relatedness among species in communities decreased as community size increased.

**Main conclusions** The majority of individual primate communities exhibit a phylogenetic structure no different from random. Yet there are across-continent differences in the phylogenetic structure of primate communities that probably result from the unique ecological and evolutionary characteristics exhibited by the endemic species found on each continent. In particular, the recent extinctions of numerous primates on Madagascar are likely responsible for the low levels of evolutionary relatedness among species in Malagasy communities.

## Keywords

Africa, Asia, biogeography, competition, extinction, macroecology, Madagascar, mammals, Neotropics, species richness.

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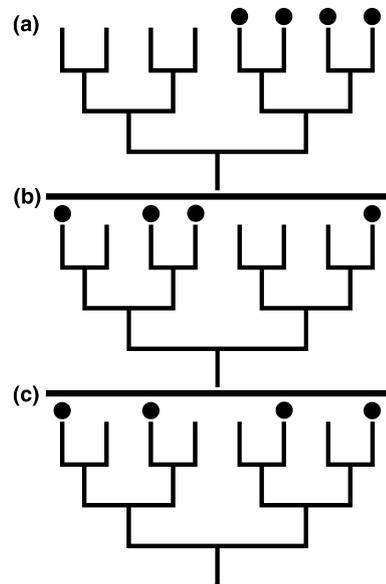
**INTRODUCTION**

One of the primary goals of community ecology is to determine factors that influence taxonomic and functional diversity within and across communities. For many years, the focus was placed on ecological factors such as resource availability and type. Although historical factors were initially often overlooked, more researchers have recently recognized the potentially important role of phylogenetic history in the assembly of communities (Losos, 1996; Grandcolas, 1998; Webb *et al.*, 2002).

It is generally accepted that a correlation exists between evolutionary relatedness and ecological similarity (Darwin, 1859; Lord *et al.*, 1995; Fleagle & Reed, 1999; Wiens & Graham, 2005; J.M.K. and K.M. Muldoon, in review). Darwin (1859) was one of the first to recognize the potential conflict between closely related taxa living in the same habitat. Some have argued that, in a habitat with limited resources, sympatric species that are in direct competition for those resources cannot co-exist stably (Lotka, 1925; Volterra, 1926; Gause, 1934). The ability for closely related species to live sympatrically in a community depends in part on divergences in their morphology or habitat use (Brown & Wilson, 1956). Darwin’s finches on the Galapagos Islands are perhaps one of the better known examples of such character displacement in closely related species (Lack, 1947). Alternatively, one or more taxa can be outcompeted by species better able to monopolize resources. Such competitive displacement is, however, a difficult theory to test, particularly in relatively long-lived animals, although there may be evidence of competitive displacement in species of the genus *Cebus* in Guyana (Lehman *et al.*, 2006).

The notion that competition plays a significant role in community ecology is a controversial one. Diamond’s (1975) analysis of bird guilds in New Guinea suggested that community structure in these taxa is based on a set of ‘assembly rules’ that are a direct consequence of competition for resources. Several authors have since argued for (e.g. Gotelli *et al.*, 1997; Gotelli & McCabe, 2002) and against (e.g. Connor & Simberloff, 1979) Diamond’s seminal paper, and although the issue of assembly rules remains unresolved, many studies continue to examine the role competition plays in community structure (Atmar & Patterson, 1993; Ganzhorn, 1997; McGill *et al.*, 2006). Some researchers present evidence that interspecific competition has little impact on community structure. Hubbell (2001) argues that species can be considered ecologically equivalent when attempting to explain broad patterns of diversity. Therefore species presence or absence in communities would not be strongly dependent on competition. Similarly, a recent simulation study by Scheffer & van Nes (2006) found that related species may coevolve towards a similar niche, occupying a similar biological position in the same community.

The incorporation of phylogenetic data into analyses of community structure allows us to better determine the role that interspecific competition plays in structuring primate



**Figure 1** Examples of the phylogenetic structure of communities: (a) phylogenetic clustering; (b) phylogenetically random; (c) phylogenetic overdispersion. Species are indicated by filled circles.

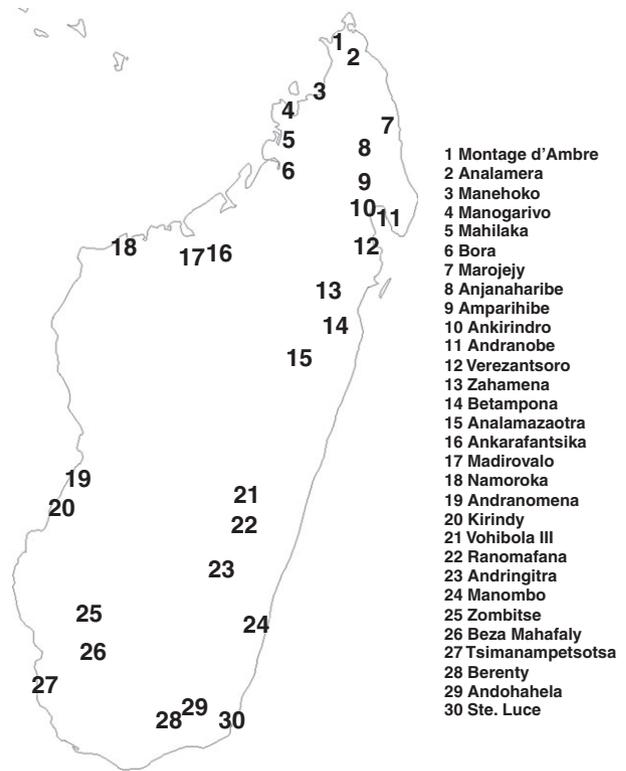
communities. Phylogenetic clustering of taxa may indicate that there is little competition among closely related species, with habitat preference being a conserved trait in a given lineage. Phylogenetic overdispersion of taxa, on the other hand, may be indicative of past competition for resources among closely related species. If there is a correlation between evolutionary relatedness and ecological similarity, then closely related species that are ecologically similar may be unable to co-exist in the same habitat due to a high degree of overlap in resource utilization, and competitive exclusion could occur. Alternatively, overdispersion could be a result of distantly related taxa that have converged on similar niche use (Webb *et al.*, 2002) (Fig. 1).

The aim of this paper is to examine the phylogenetic structure of primate communities to determine if the member species are more (or less) closely related than by chance. This will allow us to better understand the ecological and evolutionary factors that may be at work in each of these communities. We also wish to examine how phylogenetic structure may vary across continents, given the different environmental and geographical histories of each continent, variation in the ecological diversity and evolutionary trajectories of primates in each continent, and the diverse communities of non-primate taxa with which primates co-exist (Reed & Bidner, 2004). Finally, we examine the potential relationship between species richness and the phylogenetic structure of communities. Animal species richness tends to be highest in areas of high habitat quality, such as the tropics (Brown, 1995; Lomolino *et al.*, 2006). These regions contain high levels of plant species richness and diversity, which in turn drives animal richness and diversity. Based on this macroecological pattern, and the assumption that closely related taxa are more similar ecologically than distant ones, we raise two alternative

hypotheses. First, habitats of high quality may contain many closely related species due to either coevolution among species resulting in biologically similar taxa (Scheffer & van Nes, 2006), or an increase in resource availability that would reduce competition between species occupying similar niches. Consequently, this scenario would result in a positive relationship between species richness and the degree of evolutionary relatedness among species in communities. Second, habitats of high quality have a greater diversity of niches available, which allows distantly related taxa to co-exist. The second hypothesis would be supported by a negative relationship between species richness and evolutionary relatedness among species in communities.

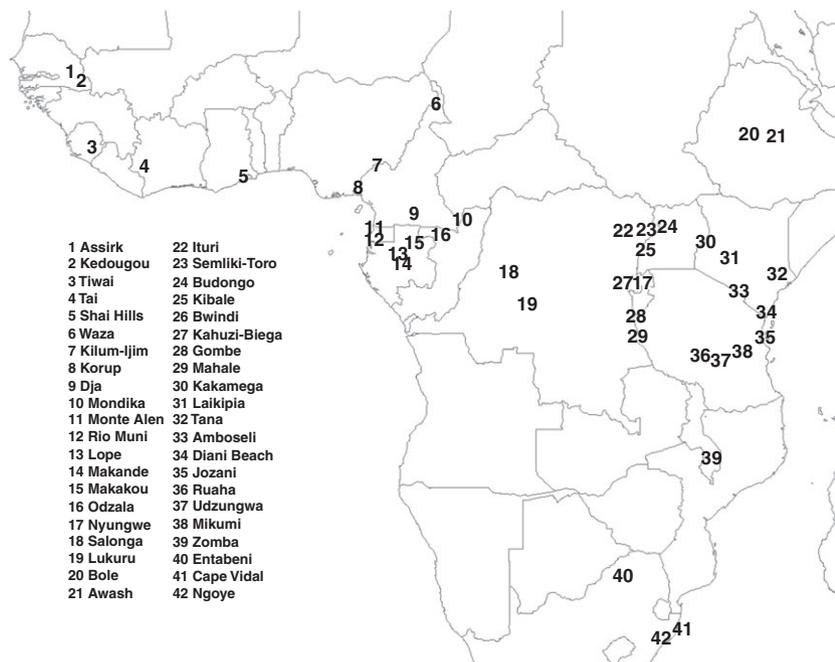
**MATERIALS AND METHODS**

We initially compiled species composition data from 154 primate communities found in four continents: Africa, Madagascar, Asia and the Neotropics (Figs 2–5; Appendices S1–S4 in Supporting Information). We define a community as the primate species that potentially can encounter each other and utilize resources at one geographical location (study site) (Reed & Bidner, 2004). Similar to previous studies (Reed & Fleagle, 1995; Fleagle & Reed, 1999), we treat Madagascar as a separate continent because of the highly diverse habitats and biota present there. When we conducted our initial analyses, it was evident that communities with three or fewer taxa produced results that were unreliable due to the large number of ties (see below), and they were therefore excluded from the analysis, as suggested by Webb *et al.* (2008). This left a total number of 120 communities. This sampling of community composition data is distributed among the continents as follows: Africa

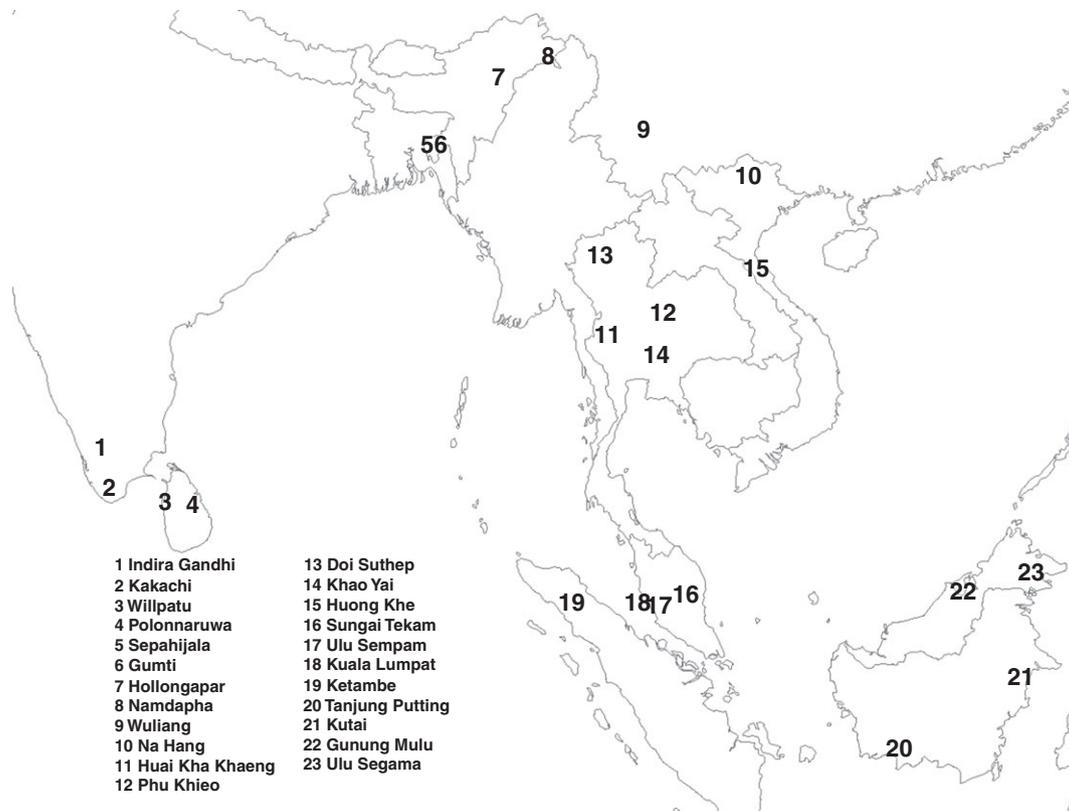


**Figure 3** Distribution of the Malagasy primate communities in this study.

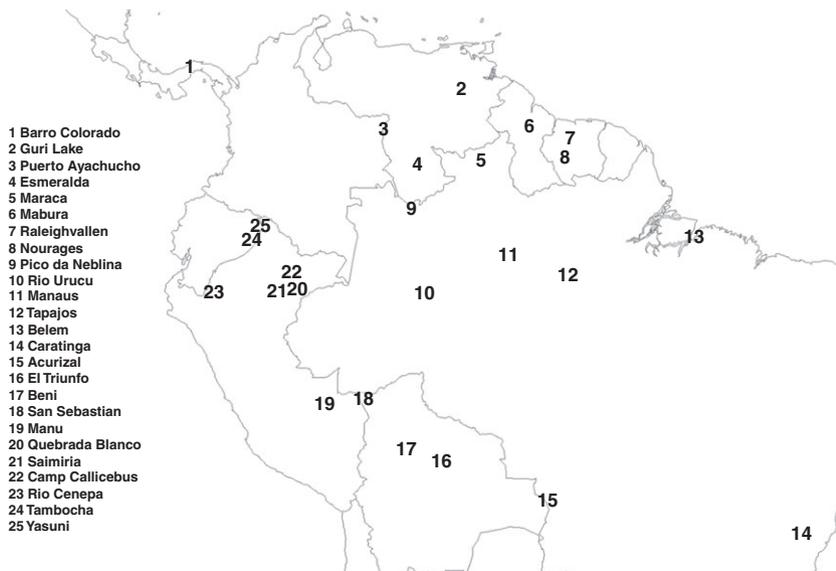
(42), Asia (23), Neotropics (25), Madagascar (30). The primate phylogeny used in the analysis was obtained from the mammal supertree published by Bininda-Emonds *et al.* (2007). The primate taxonomy used in this phylogeny follows the recent



**Figure 2** Distribution of the African primate communities in this study.



**Figure 4** Distribution of the Asian primate communities in this study.



**Figure 5** Distribution of the Neotropical primate communities in this study.

trend toward a ‘splitter’ arrangement, resulting from elevating subspecies to species status and considering newly discovered taxa as new species. This practice has been especially common with Malagasy and Neotropical primates (e.g. Mittermeier *et al.*, 2006; Rylands & Mittermeier, 2009). Although many of these ‘new’ taxa are not included in our dataset, there are some cases where previously acknowledged subspecies are treated as full species. Therefore, in addition to conducting analyses

using recent taxonomy (as followed by Bininda-Emonds *et al.*, 2007), we conducted an additional set of analyses for Malagasy and Neotropical primate communities utilizing a more traditional (‘lumper’) taxonomy presented by Fleagle (1999).

In order to determine whether primate communities are non-random in terms of mean evolutionary relatedness, a randomization model was employed to compare observed phylogenetic distance of species in communities compared

with randomized values drawn from the entire regional pool of species. We chose the program `PHYLOCOM` to conduct these analyses (Webb *et al.*, 2008), as this software package was created for the express purpose of exploring community structure from a phylogenetic perspective. It has been used in several studies of plant (Webb, 2000; Cavender-Bares *et al.*, 2004, 2006) and animal (Horner-Devine & Bohannan, 2006; Cardillo *et al.*, 2008; Cooper *et al.*, 2008) communities.

For each continent, we calculated two indices to provide a measure of the phylogenetic distance of a community's member species. Both measures are standardized to take into account the degree of relatedness among all species in the sampling pool. The first index, the net relatedness index (NRI), measures the mean phylogenetic distance (MPD) between all species pairs in a community relative to the mean phylogenetic distance of all taxa in the species pool. It is calculated as follows:

$$\text{NRI} = -1 \times (\text{MPD}_{\text{sample}} - \text{MPD}_{\text{rnd sample}}) / \text{sdMPD}_{\text{rnd sample}}$$

where  $\text{MPD}_{\text{sample}}$  is the observed mean phylogenetic distance between all species pairs in a given community,  $\text{MPD}_{\text{rnd sample}}$  is the mean phylogenetic distance between all species pairs in the randomized communities, and  $\text{sdMPD}_{\text{rnd sample}}$  is the standard deviation of the phylogenetic distance in the randomized communities. Negative values result when the observed MPD is greater than expected, and thus are indicative of phylogenetic overdispersion. Conversely, a positive NRI value indicates that the MPD is lower than expected and that phylogenetic clustering of taxa is occurring. Values near zero indicate a phylogenetically random assemblage of species. The second index we calculated was the nearest taxon index (NTI). While this is also a measure of phylogenetic structure in a community, it is based on the mean nearest phylogenetic neighbour distance (MNND) rather than on the mean phylogenetic distance between all species pairs in a community. This index allows us to address whether the most closely related species in a community are more related than expected by chance alone. It is calculated in a similar fashion to NRI, with the MNND values substituted for the MPD values as follows:

$$\text{NTI} = -1 \times (\text{MNND}_{\text{sample}} - \text{MNND}_{\text{rnd sample}}) / \text{sdMNND}_{\text{rnd sample}}$$

Negative values indicate that closely related taxa do not co-occur, while positive values indicate that they co-occur more than expected by chance alone. Similarly to NRI, values near zero indicate a phylogenetically random assemblage of species.

We used `MESQUITE` (Maddison & Maddison, 2007) to create the Newick form of the phylogeny, which is the required format for the `PHYLOCOM` program. For each continent, null communities were generated by sampling (without replacement) only those species that are present in at least one primate community in each continent. The species richness for each sample was maintained and a total of 9999 randomizations were conducted to generate *P* values. Although Cooper

*et al.* (2008) and Cardillo *et al.* (2008) showed that the spatial extent (and, by proxy, the species pool size) had little effect on the phylogenetic structure of mammal communities, we conducted two sets of analyses using different species pools. The first species pool was at the continental level, comprising all species in our dataset for a particular continent. The second set of analyses utilized a regional species pool. Major biogeographical regions (areas of endemism) are present within each continent and represent different evolutionary histories and/or habitats. Our biogeographical regions were based on the results from Kamilar (2009), who examined biogeographical variation in the taxonomic structure of primate communities using unweighted pair group method with arithmetic mean (UP-GMA) cluster analyses and a similar dataset to our current study. Within each continent, Kamilar (2009) found biogeographical zones (areas of endemism), which consisted of communities that were more taxonomically similar to each other compared with communities in other biogeographical zones. We defined the following regions within each continent: (1) Africa: East, West, and Central, (2) Madagascar: East and West, (3) Asia: Mainland Southeast and Sunda Shelf, and (4) Neotropics: Central Amazon, Western Amazon and Guyana Shield. To have a species pool large enough to obtain reliable results, we analysed only regions that contained at least five communities. Therefore not all communities were included in the regional species pool analyses.

We used a least-squares linear regression to examine the possible relationship between species richness and the phylogenetic structure of communities in each continent. Linear regression models were tested with and without potential outliers in the datasets. We used Q–Q plots to examine the degree of normality of our residuals. In addition, we identified outliers as any data point with a studentized residual of  $\pm 3.0$  and/or a Cook's distance of  $> 1.0$ .

We performed Kruskal–Wallis tests to determine whether our measures of community phylogenetic structure differed across continents. This nonparametric test was chosen because the assumptions of parametric tests can be relaxed without sacrificing a large amount of statistical power (Quinn & Keough, 2002). Regression and Kruskal–Wallis analyses were conducted in R ver. 2.6.2 and STATISTICA ver. 6.0.

## RESULTS

### Phylogenetic structure of individual primate communities

We found that most individual primate communities exhibited negative NRI and NTI values, regardless of the species pool or taxonomy utilized (Appendices S1–S5). Negative values indicate that species found in the same community are less closely related to each other than to a random assemblage of species. This is true whether we measured the average phylogenetic distance between all species pairs in a community (NRI) or the phylogenetic distance between the most closely related species in a community (NTI). Although most values were negative, it

**Table 1** The percentage of primate communities that are phylogenetically random, overdispersed and clustered based on (a) the net relatedness index; (b) the nearest taxon index.

| Continent  | Taxonomy | Species pool | Random (%) | Overdispersed (%) | Clustered (%) | No. of communities |
|------------|----------|--------------|------------|-------------------|---------------|--------------------|
| (a)        |          |              |            |                   |               |                    |
| Africa     | Splitter | Continental  | 95.2       | 4.8               | 0.0           | 42                 |
| Africa     | Splitter | Regional     | 87.1       | 10.3              | 2.6           | 39                 |
| Asia       | Splitter | Continental  | 100.0      | 0.0               | 0.0           | 23                 |
| Asia       | Splitter | Regional     | 89.5       | 10.5              | 0.0           | 19                 |
| Madagascar | Splitter | Continental  | 87.0       | 13.0              | 0.0           | 30                 |
| Madagascar | Splitter | Regional     | 96.7       | 3.3               | 0.0           | 30                 |
| Madagascar | Lumper   | Continental  | 93.3       | 6.7               | 0.0           | 30                 |
| Madagascar | Lumper   | Regional     | 96.7       | 3.3               | 0.0           | 30                 |
| Neotropics | Splitter | Continental  | 96.0       | 4.0               | 0.0           | 25                 |
| Neotropics | Splitter | Regional     | 100.0      | 0.0               | 0.0           | 22                 |
| Neotropics | Lumper   | Continental  | 96.0       | 4.0               | 0.0           | 25                 |
| Neotropics | Lumper   | Regional     | 96.5       | 4.5               | 0.0           | 22                 |
| (b)        |          |              |            |                   |               |                    |
| Africa     | Splitter | Continental  | 100.0      | 0.0               | 0.0           | 42                 |
| Africa     | Splitter | Regional     | 100.0      | 0.0               | 0.0           | 39                 |
| Asia       | Splitter | Continental  | 91.3       | 8.7               | 0.0           | 23                 |
| Asia       | Splitter | Regional     | 89.5       | 10.5              | 0.0           | 19                 |
| Madagascar | Splitter | Continental  | 63.3       | 36.7              | 0.0           | 30                 |
| Madagascar | Splitter | Regional     | 86.7       | 13.3              | 0.0           | 30                 |
| Madagascar | Lumper   | Continental  | 63.4       | 33.3              | 3.3           | 30                 |
| Madagascar | Lumper   | Regional     | 90.0       | 10.0              | 0.0           | 30                 |
| Neotropics | Splitter | Continental  | 96.0       | 4.0               | 0.0           | 25                 |
| Neotropics | Splitter | Regional     | 100.0      | 0.0               | 0.0           | 22                 |
| Neotropics | Lumper   | Continental  | 96.0       | 4.0               | 0.0           | 25                 |
| Neotropics | Lumper   | Regional     | 100.0      | 0.0               | 0.0           | 22                 |

**Table 2** Results of Wilcoxon tests examining differences in net relatedness index (NRI) and nearest taxon index (NTI) scores using lumpers versus splitter taxonomies for Malagasy and Neotropical primate communities. Lower scores indicate larger phylogenetic distances among taxa.

| Continent  | Species pool | Community measure | Z    | P      | n  | Splitter mean ± SD | Lumper mean ± SD |
|------------|--------------|-------------------|------|--------|----|--------------------|------------------|
| Madagascar | Continental  | NRI               | 4.57 | <0.001 | 30 | -0.782 ± 0.730     | -0.714 ± 0.767   |
| Madagascar | Regional     | NRI               | 1.16 | 0.245  | 30 | -0.570 ± 0.748     | -0.509 ± 0.820   |
| Madagascar | Continental  | NTI               | 4.78 | <0.001 | 30 | -1.48 ± 1.08       | -1.39 ± 1.09     |
| Madagascar | Regional     | NTI               | 2.17 | 0.030  | 30 | -1.02 ± 0.957      | -0.970 ± 0.945   |
| Neotropics | Continental  | NRI               | 3.11 | 0.002  | 25 | -0.462 ± 0.661     | -0.481 ± 0.645   |
| Neotropics | Regional     | NRI               | 2.26 | 0.024  | 22 | -0.320 ± 0.751     | -0.343 ± 0.718   |
| Neotropics | Continental  | NTI               | 1.01 | 0.313  | 25 | -0.474 ± 0.703     | -0.477 ± 0.715   |
| Neotropics | Regional     | NTI               | 0.93 | 0.354  | 22 | -0.358 ± 0.680     | -0.332 ± 0.708   |

is important to note that only a relatively small proportion of communities exhibited statistically significant NRI and/or NTI values (Table 1a,b). Malagasy communities had the highest proportion of communities that exhibited significant or near-significant NTI values.

We found statistically significant differences in both measures of the phylogenetic structure of Malagasy communities when using different taxonomic schemes. For Neotropical communities, different taxonomies produced significantly different NRI values only. Although we found statistically significant effects of taxonomic scheme, the magnitudes of the

differences were quite small. For instance, when using a continental species pool in Madagascar, the mean NTI value using a splitter taxonomy was -1.48 and that using a lumpers taxonomy was -1.39 (Table 2).

Quantifying the phylogenetic structure of communities was affected by species pool size for some continents and not others (Table 3). We found a significant difference in the average phylogenetic relatedness between all species pairs (NRI) in Malagasy and Neotropical communities when we used continental versus regional species pools. We also found a significant difference in phylogenetic distance between the

**Table 3** Results of Wilcoxon tests examining the differences in net relatedness index (NRI) and nearest taxon index (NTI) scores using continental versus regional primate species pools. Lower scores indicate larger phylogenetic distances among taxa.

| Continent  | Community measure | Z     | P      | n  | Continental mean $\pm$ SD | Regional mean $\pm$ SD |
|------------|-------------------|-------|--------|----|---------------------------|------------------------|
| Africa     | NRI               | 0.962 | 0.336  | 39 | -0.674 $\pm$ 0.489        | -0.592 $\pm$ 0.935     |
| Africa     | NTI               | 5.09  | <0.001 | 39 | -0.250 $\pm$ 0.737        | -0.053 $\pm$ 0.766     |
| Madagascar | NRI               | 4.17  | <0.001 | 30 | -0.782 $\pm$ 0.730        | -0.570 $\pm$ 0.748     |
| Madagascar | NTI               | 4.60  | <0.001 | 30 | -1.48 $\pm$ 1.08          | -1.02 $\pm$ 0.957      |
| Asia       | NRI               | 1.65  | 0.099  | 19 | -0.471 $\pm$ 0.581        | -0.364 $\pm$ 0.617     |
| Asia       | NTI               | 0.080 | 0.936  | 19 | -0.713 $\pm$ 0.782        | -0.748 $\pm$ 0.802     |
| Neotropics | NRI               | 3.07  | 0.002  | 22 | -0.462 $\pm$ 0.661        | -0.320 $\pm$ 0.751     |
| Neotropics | NTI               | 0.698 | 0.485  | 22 | -0.474 $\pm$ 0.703        | -0.358 $\pm$ 0.680     |

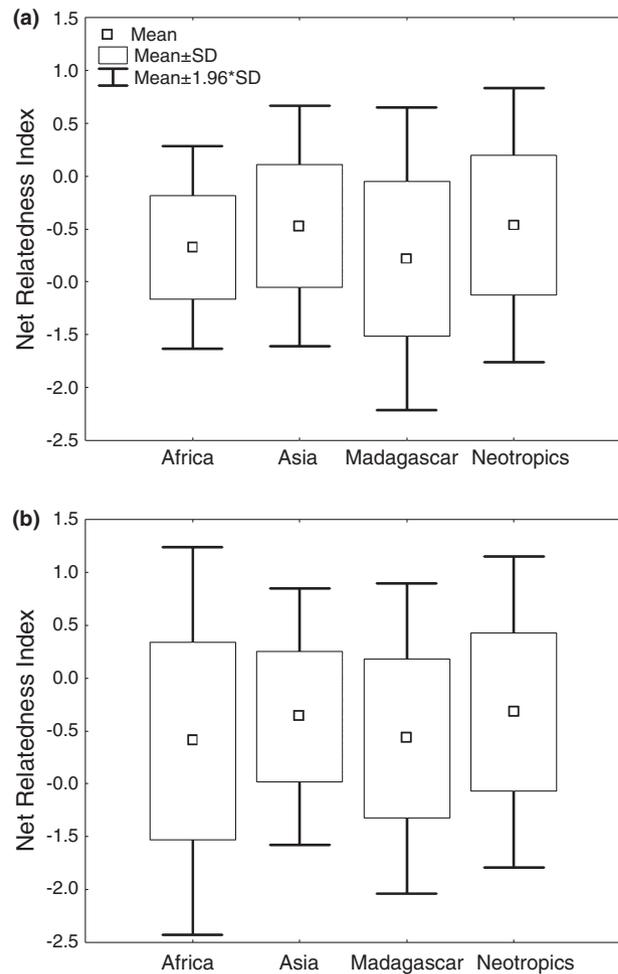
most closely related species (NTI) in African and Malagasy communities using continental versus regional species pools. In all cases, using a continental species pool produced lower NRI and NTI values compared with a regional species pool, indicating that species in communities were more distantly related.

### Comparing the phylogenetic structure of primate communities within and across continents

We found that the mean phylogenetic distance between all species pairs in communities (NRI) did not differ significantly across continents, regardless of the species pool used (continental pool:  $P = 0.068$  and regional pool:  $P = 0.166$ ) (Fig. 6). In contrast, we found an across-continent difference in the phylogenetic distance between the most closely related species in communities (NTI) using both a continental (Kruskal–Wallis  $\chi^2 = 29.10$ , d.f. = 3,  $P < 0.001$ ) and regional species pool (Kruskal–Wallis  $\chi^2 = 23.13$ , d.f. = 3,  $P < 0.001$ ) (Fig. 7). We found the highest NTI values in Africa, indicating that communities often contained several closely related species. We also found that Asian and Neotropical communities exhibited relatively moderate NTI values, and Malagasy communities displayed the lowest scores.

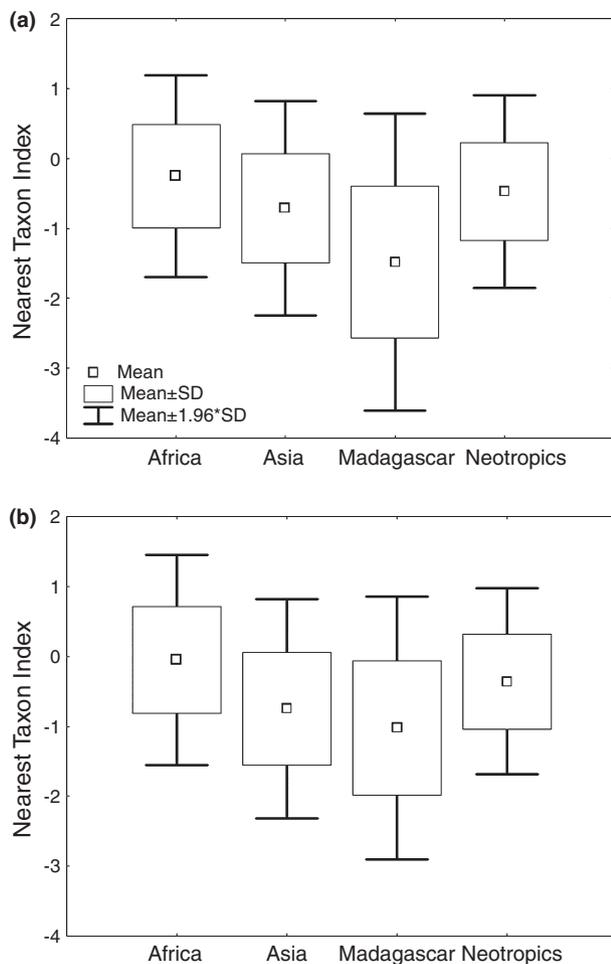
When examining the relationship between species richness and the phylogenetic structure of communities using a continental species pool, we found significant results for Africa, Asia and Madagascar (see Appendix S6a–c for more details). In Africa, there is a significant negative relationship between species richness and the degree of relatedness among species ( $r^2 = 0.141$ ,  $P = 0.014$ , d.f. = 40). Removing the outlier community, Ituri, yielded a better model ( $r^2 = 0.400$ ,  $P < 0.001$ , d.f. = 39). As the number of taxa in communities increases, the average relatedness of the species in these communities decreases. The remaining continents did not exhibit a statistically significant relationship between community species richness and NRI (Table 4a).

A similar pattern was found between the nearest taxon index and community species richness in Asia ( $r^2 = 0.373$ ,  $P = 0.002$ , d.f. = 21) and Madagascar ( $r^2 = 0.329$ ,  $P < 0.001$ , d.f. = 28). A better regression model was produced when we removed the outlier community Mt d'Ambre from the Malagasy dataset ( $r^2 = 0.380$ ,  $P < 0.001$ , d.f. = 27). As com-



**Figure 6** Distribution of net relatedness index (NRI) values for primates compared across continents. (a) NRI values were calculated using a continental species pool and a 'splitter' taxonomy for the Neotropical and Malagasy primates. Kruskal–Wallis  $\chi^2 = 7.12$ , d.f. = 3,  $P = 0.068$ . (b) NRI values were calculated using a regional species pool and a 'splitter' taxonomy for the Neotropical and Malagasy primates. Kruskal–Wallis  $\chi^2 = 5.08$ , d.f. = 3,  $P = 0.166$ .

munity species richness increases, the nearest taxon index of communities decreases. Communities in Africa and the Neotropics did not exhibit a statistically significant



**Figure 7** Distribution of nearest taxon index (NTI) values for primates compared across continents. (a) NTI values were calculated using a continental species pool and a ‘splitter’ taxonomy for the Neotropical and Malagasy primates. Kruskal–Wallis  $\chi^2 = 29.10$ , d.f. = 3,  $P < 0.001$ . (b) NTI values were calculated using a regional species pool and a ‘splitter’ taxonomy for the Neotropical and Malagasy primates. Kruskal–Wallis  $\chi^2 = 23.13$ , d.f. = 3,  $P < 0.001$ .

relationship between species richness and NTI (Table 4b). All regression analyses produced similar results when we used a regional species pool for calculating both measures of the phylogenetic structure of communities.

**DISCUSSION**

The results of our analyses examining the phylogenetic structure of primate communities are mixed. First, using two metrics of species relatedness, we found that the majority of individual primate communities are comprised of phylogenetically random species assemblages compared with regional or continental species pools. However, there are some communities in Africa and Madagascar that show significantly low net relatedness values, indicating that the community comprises

**Table 4** Results of regression analyses examining the relationship between primate species richness and (a) net relatedness index (NRI); (b) nearest taxon index (NTI).

| (a)         |              |                   |       |        |     |
|-------------|--------------|-------------------|-------|--------|-----|
| Dataset     | Species pool | Standardized beta | $r^2$ | $P$    | $n$ |
| Africa*     | Continental  | -0.632            | 0.400 | <0.001 | 41  |
| Africa*     | Regional     | -0.717            | 0.513 | <0.001 | 38  |
| Asia        | Continental  | -0.278            | 0.077 | 0.199  | 23  |
| Asia        | Regional     | -0.361            | 0.130 | 0.129  | 20  |
| Madagascar† | Continental  | 0.086             | 0.007 | 0.656  | 29  |
| Madagascar  | Regional     | 0.211             | 0.045 | 0.263  | 30  |
| Neotropics‡ | Continental  | 0.294             | 0.086 | 0.163  | 24  |
| Neotropics‡ | Regional     | 0.282             | 0.080 | 0.215  | 24  |

\*Does not include the outlier community Ituri.

†Does not include the outlier community Mt d’Ambre.

‡Does not include the outlier community Camp Callicebus.

| (b)         |              |                   |       |        |     |
|-------------|--------------|-------------------|-------|--------|-----|
| Dataset     | Species pool | Standardized beta | $r^2$ | $P$    | $n$ |
| Africa      | Continental  | -0.127            | 0.016 | 0.423  | 42  |
| Africa      | Regional     | -0.147            | 0.022 | 0.370  | 39  |
| Asia        | Continental  | -0.611            | 0.373 | 0.002  | 23  |
| Asia        | Regional     | -0.534            | 0.285 | 0.019  | 20  |
| Madagascar* | Continental  | -0.616            | 0.380 | <0.001 | 29  |
| Madagascar  | Regional     | -0.298            | 0.089 | 0.110  | 30  |
| Neotropics  | Continental  | 0.278             | 0.077 | 0.178  | 25  |
| Neotropics  | Regional     | 0.255             | 0.065 | 0.253  | 25  |

\*Does not include the outlier community Mt d’Ambre.

species that are more distantly related than by chance. There may be several reasons to explain the phylogenetically random structure of many communities. Many species may be ecologically flexible, and therefore may not have specific habitat requirements (Kamilar, 2009). Along the same lines, Hubbell’s (2001) neutral theory of biodiversity suggests that species can be treated as ecologically equivalent, with interspecific competition playing a lesser role in explaining broad patterns of diversity. Additionally, several field studies focused on primate communities showed that many species are able to reduce interspecific competition with closely related taxa through habitat partitioning and/or switching dietary resources during times of preferred food scarcity (Gautier-Hion *et al.*, 1983; Porter, 2001; Buzzard, 2006). Finally, studies examining the phylogenetic structure of communities rely on the assumption that there is a significant degree of phylogenetic signal (the degree to which a trait is correlated to a phylogeny) in biological traits related to interspecific competition (Losos, 2008). Relatively few studies have examined the degree of phylogenetic signal in the biological traits of most species, with existing studies finding mixed results (Blomberg *et al.*, 2003; Knouft *et al.*, 2006; Ossi & Kamilar, 2006; Kamilar *et al.*, 2008).

There are some important exceptions to the random phylogenetic pattern, especially in Madagascar. In Madagascar, numerous communities have significantly low NTI values, indicating that the most closely related species in communities are phylogenetically distinct. Because the NTI measures solely the nearest phylogenetic neighbour for each member species, it may be a better indicator of potential competition in a community, assuming biological traits are evolutionarily conserved (Webb *et al.*, 2002; Kraft *et al.*, 2007). It can be compared with the species-to-genus ratio approach that was for many years a focus of community ecologists, prior to the recognition of the importance of phylogeny in community ecology (Simberloff, 1970; Tokeshi, 1991).

In Africa, Asia and Madagascar, a negative correlation exists between the number of taxa within a community and the degree of relatedness of community members. Phylogenetic overdispersion such as this is indicative of one of several factors that are not mutually exclusive. Past competition is one interpretation. Given the fact that closely related species tend to be ecologically similar (Darwin, 1859; Harvey & Pagel, 1991; Fleagle & Reed, 1996; Wiens & Graham, 2005), one would expect that competition over finite resources would result in the exclusion of closely related species. Alternatively, phylogenetic overdispersion could be the result of convergence by distantly related species on the same habitat (Webb *et al.*, 2002), which again may reflect the role of competition over resources, as distantly related species tend to have a smaller degree of overlap in resource use than closely related species. Another explanation altogether could be that overdispersion is a result of recent extinctions, whereby there has been insufficient time for extant species to radiate into newly vacant ecological niches. Finally, there is a positive relationship between species richness and rainfall (Reed & Fleagle, 1995; Kay *et al.*, 1997), and rainfall is positively correlated with plant productivity (up to *c.* 2700 mm yr<sup>-1</sup>) (Kay *et al.*, 1997). These highly productive sites are often also associated with high levels of plant diversity, and therefore may contain more ecological niches compared with poor sites. Consequently, the lower phylogenetic relatedness values in species-rich sites may be the result of more available niches in the habitat, in turn, being filled by a biologically (and phylogenetically) diverse set of species.

### African communities

Of the 39 African communities included in the regional species pool analysis, all but one consisted of phylogenetically overdispersed or random sets of species. The community of Ituri is therefore anomalous in having a significantly positive NRI value, which indicates that its species are very closely related. With 17 primate species, it is one of the world's richest primate communities (Chapman *et al.*, 1999). Six species of guenons are known to live sympatrically here, as well as several other groups of closely related species, including three colobus monkeys. As the cercopithecoïd radiation is more recent than that of the prosimians or apes, it is the abundance of members of this clade that generated a relatively high degree of

phylogenetic clustering compared with most other African communities. Additionally, Africa was the only region to have higher mean NTI values compared with NRI values, indicating that closely related species are often found together in the same community (Kamilar, 2009; Kamilar *et al.*, 2009). African communities do indeed have a large number of sympatric congeners, particularly the guenons, which can number as many as six species at a given site.

### Malagasy communities

Malagasy communities stand out in this analysis in having communities with the greatest phylogenetic distance. This is particularly true of the occurrence (or lack thereof) of closely related taxa. The mean value of the parameter (NTI) was striking, being nearly six times that of Africa. Although there are distinct species compositions in eastern versus western Malagasy communities (Ganzhorn, 1998; Kamilar, 2009), our phylogenetic measures of community structure do not differ greatly between the deciduous and evergreen forests.

Any analysis that investigates evolutionary relatedness in the primates of Madagascar must take into consideration the recent extinction of at least 16 species of lemurs. Although only one of the extinct species (*Daubentonia robusta*) has an extant congener, several extinct genera contained more than one species, and many of these were probably sympatric (Godfrey *et al.*, 1997). For instance, *Megaladapis edwardsi* and *Megaladapis madagascariensis* co-occurred across the south and south-west (Godfrey *et al.*, 1997). In addition, three closely related species of sloth lemur (of different genera but all from the family Megaladapidae) were sympatric in central Madagascar, while three additional species of sloth lemur were sympatric in the north.

Because many of the subfossil lemurs were geographically widespread and were very different from lemurs of today in terms of body size, locomotion and dietary patterns, we can be fairly confident that many of them lived sympatrically with living species. It is highly probable that Madagascar's extremely low occurrence of sympatric congeners reflects the absence of the recently extinct subfossil lemurs. Therefore we argue that phylogenetic overdispersion could also be a result of a large number of recent extinctions whereby there has been insufficient time for extant taxa to radiate into newly vacant niches. Although recent primate extinctions have occurred in other regions (e.g. Pleistocene extinctions of *Theropithecus* species in Africa; Jablonski, 1993), the relative proportion of species lost is substantially greater in Madagascar. Sufficient data documenting recent extinctions, as found in the Malagasy primates, would be needed to justify this mechanism shaping community structure in other continents.

### Asian communities

While the majority of communities in Asia have member species that are somewhat distantly related, Hologapar, Huong Khe and Wuliang are the exceptions. The species in

each of these three assemblages are phylogenetically clustered as measured by both indices. What these communities have in common is a lack of lorises and tarsiers as well as orangutans. Instead they contain one gibbon species, one or more colobine, and one or more cercopithecine. Because of the absence of prosimians and great apes, the mean phylogenetic distance of each pair of species is relatively low and thus the overall relatedness of member species is high.

### Neotropical communities

Compared with other continents, member species of Neotropical communities tend to be more closely related than those of the other three biogeographical regions. This result is probably related to the findings of Fleagle & Reed's (1996) study, which showed that Neotropical primates exhibit the least amount of ecological diversity of all regions. While it could be assumed that the low degree of phylogenetic diversity is simply due to a lack of prosimians and apes in the Neotropics, this is in fact not the case, as the PHYLOCOM program samples only from the continental species pool rather than from all primate taxa.

Several Neotropical communities contain sympatric species from the family Callitrichidae. Although members of this family are closely related and occupy similar ecological niches (broadly defined), previous research has shown that species of this family often benefit from living sympatrically. Co-existing callitrichid species may gain advantages related to food acquisition, predator defence, and/or resource defence (Heymann & Buchanan-Smith, 2000).

It is also important to note that Neotropical primates are less biologically diverse compared with those found on other continents. Primates are believed to have first colonized the Neotropics approximately 30 Ma (Takai *et al.*, 2000). The adaptive radiation of platyrrhines was similar to that of the lemurs in that it was explosive upon their colonization of the New World, although it was a younger and more ecologically uniform radiation (Fleagle, 1999; Fleagle & Reed, 2004). In contrast to the other continents, Neotropical primates are highly conserved ecologically. There are few nocturnal species, few folivores, and no terrestrial species. Because of the relatively low ecological diversity within the radiation, there is a relatively weak relationship between evolutionary distance and ecological distance (Fleagle & Reed, 1999). This may contribute to the overwhelmingly random phylogenetic structure of Neotropical primate communities.

Finally, the lack of correlation in the Neotropics between phylogenetic distance and species richness may be related to the fact that small communities in the Neotropics tend to have variable species compositions. Most small Neotropical communities (e.g. of fewer than six species) contain at least one *Cebus* and one *Alouatta* species, yet the remaining species may differ quite dramatically in terms of their phylogenetic affinities. Small communities in Central America may contain *Saguinus* and *Saimiri* species, which are relatively closely related to *Cebus*. In contrast, small primate communities in the

Guyana Shield region often include species from the subfamily Pitheciinae, which are more distantly related to *Cebus* (and *Alouatta*). This is in contrast to Africa, where small communities tend to consist of the same species (e.g. baboons, vervets, galagos): African sites with low species richness are generally unfavourable in terms of habitat quality and therefore can support only generalist species.

### Between-continent variation in the phylogenetic structure of primate communities

Our results show that there is a significant among-continent difference in the phylogenetic structure of primate communities in terms of average phylogenetic distance between species pairs. Fleagle & Reed (1996) found a similar pattern when they examined the ecological niche space occupied by primate communities in all four biogeographical regions. The authors found that the ecospace occupied by communities within a continent were remarkably similar to one another, yet very diverse from the ecospace occupied by communities in other continents.

We found that the phylogenetic structures of African and Asian primate communities are quite similar to one another. This is perhaps not surprising, given that these two continents share many of the same families (Lehman & Fleagle, 2006). However, the underlying causes influencing community structure in the two continents is probably dissimilar. Africa was the only continent to have a higher NTI than NRI value, which reflects the relatively high proportion of sympatric congeners found in communities from this continent. While competition with other primates has probably been an influencing factor in Asian primate communities, it is possible that there is a greater degree of competition with non-primate mammals than in the other continents (Ganzhorn, 1999).

### Previous studies of the phylogenetic structure of mammal communities

Recent studies of the phylogenetic structure of mammalian communities have yielded similar results to ours. Cardillo *et al.* (2008) examined mammal communities on islands and found that most assemblages displayed phylogenetic patterns that were not significantly different from random. The remaining mammalian communities exhibited both phylogenetically overdispersed and clustered communities, though no primate communities were significantly clustered. Similar results were found in a study by Cooper *et al.* (2008), investigating the phylogenetic structure of three mammal groups: Neotropical primates, North American ground squirrels and Australian marsupials. It is important to note some methodological differences between these two studies and our paper. First, the datasets of both Cardillo *et al.* (2008) and Cooper *et al.* (2008) included communities with only three species, yet did not report whether these communities produced unstable results, as may be indicated by numerous ties generated from the

randomization analyses. Second, these studies utilized different-sized species pools based on various spatial scales, from 150 to 1000 km (with larger species pools existing at larger spatial scales), yet they were based solely on spatial extent, not biogeographical regions. Both studies found little effect of species pool size on the phylogenetic structure of communities. Our use of species pools based on biogeographical regions within continents versus the entire continental scale did in fact produce statistically significant differences in the phylogenetic composition of primate communities. The discrepancy between our results and previous findings is likely to be due to our use of biogeographical zones (areas of endemism; Kamilar, 2009), which better reflects differences in the evolutionary history of taxa, and therefore the phylogenetic structure of communities.

## CONCLUSIONS

In summary, we found that most primate communities exhibit a phylogenetic structure that is no different from random. This result supports previous analyses of the phylogenetic structure of mammal communities. We also showed that the average degree of relatedness among species in communities differed across continents. In particular, Malagasy primate communities contain an assemblage of primates that are relatively distantly related compared with communities on other continents. This may be due to a combination of interspecific competition between Malagasy primate species in the past, and the extinction of a significant proportion of species in the past few thousand years. In addition, in three of the four continents, we found that there is a negative relationship between community size and the degree of relatedness of species in communities. This supports our prediction that habitats of high quality have a greater diversity of niches available, which allows larger numbers of distantly related taxa to co-exist. This finding may also support the idea that interspecific competition increases as community size increases. The latter point is contingent on Webb *et al.*'s (2002) assumption that strong interspecific competition in the past can produce modern communities that contain few closely related species.

We also found that the phylogenetic structure of communities sometimes differs when using different-sized species pools, which were based on areas of endemism as opposed to spatial scale without reference to species ranges. This finding differed from those of previous studies that based species pool size strictly on spatial extent, for example, a species pool would include all the species within a 100, 250 and 1000 km radius of the community in question. Therefore we suggest that using different-sized species pools should be based on biogeographical regions (areas of endemism) instead of different spatial scales alone. In view of the findings presented here, we conclude that accounting for the unique ecological and evolutionary patterns in each continent is essential for a better understanding of the structure of primate communities.

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## SUPPORTING INFORMATION

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

**Appendix S1** PHYLOCOM analyses using the splitter taxonomy and continental species pool dataset.

**Appendix S2** PHYLOCOM analyses using the splitter taxonomy and regional species pool dataset.

**Appendix S3** PHYLOCOM analyses using the lumpers taxonomy and continental species pool dataset.

**Appendix S4** PHYLOCOM analyses using the lumpers taxonomy and regional species pool dataset.

**Appendix S5** The effect of taxonomy and species pool size for quantifying the phylogenetic structure of communities.

**Appendix S6** The relationship between species richness and the phylogenetic structure of primate communities.

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