Environmental and Geographic Correlates of the Taxonomic Structure of Primate Communities

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ABSTRACT   Previous research has shown that both environmental and historical factors influence the taxonomic structure of animal communities; yet, the relative importance of these effects is not known for primates. Environmental characteristics shape the possible niches in a community, providing suitable habitats for some species and not others. Therefore, communities found in similar environments should display similar species compositions. Additionally, geography may be viewed as a surrogate for historical processes. For instance, as the geographic distance between communities increases, dispersal between sites is more limited, and the probability of historical vicariance increases. Therefore, communities in close proximity to each other should exhibit similar species compositions. The geographic location, environmental characteristics, and species composition of 168 primate communities were gathered from the literature. Canonical correspondence analyses were conducted to examine the relative effects of geographic distance and environmental variables on the taxonomic structure of communities. In addition, UPGMA cluster analyses were conducted to better visualize the taxonomic similarity of communities. Spatial variables were significant predictors of community structure in all regions. Rainfall patterns explained African, Malagasy, and Neotropical community structure. In addition, maximum temperature was also correlated with community structure in Madagascar and the Neotropics. No climatic variables predicted Asian community structure. These results demonstrate that both historical and environmental factors play a significant role in structuring modern primate communities; yet, the importance of environmental factors depend on the region in question. Am J Phys Anthropol 000:000–000, 2009.   © 2008 Wiley-Liss, Inc.

Although recent studies have shown that both environmental and historical factors influence community structure (Harcourt, 2000; Chase, 2003; Reed and Bidner, 2004; Graham et al., 2005; Ricklefs, 2006), most primate community ecology research has been conducted from either an ecological or evolutionary perspective. The most common studies have focused on the role of abiotic factors such as rainfall and temperature in shaping various aspects of communities, including local species richness (Reed and Fleagle, 1995; Kay et al., 1997), often without explicitly accounting for the particular species in the community. With regards to animal communities, climatic factors shape the abundance and diversity of vegetation in the environment, and this in turn sets the stage for the possible animal taxa inhabiting a particular area based on the niches available (Terborgh and van Schaik, 1987; Kay et al., 1997).

Broad-scale studies of primate communities have shown a positive relationship between annual rainfall and the number of primate species at a site in Africa, the Neotropics, and Madagascar (Terborgh and van Schaik, 1987; Reed and Fleagle, 1995; Peres and Janson, 1999). The driving factor behind this relationship is probably plant productivity, which increases with rainfall, and therefore provides a greater abundance of resources for primates to use (Reed and Fleagle, 1995; Kay et al., 1997). Additional studies focusing on the Neotropics and Southeast Asia have found that the relationship between rainfall and primate diversity and biomass is not linear (Kay et al., 1997; Gupta and Chivers, 1999). For these areas, when a more representative sample of communities is included, primate diversity decreases in high rainfall sites with over 2,500 mm of rain per year. This negative relationship in high rainfall communities is probably due to soil leaching and decreased plant productivity.

The quantitative examination of evolutionary history has not been a major focus of community ecology research until recently (Ricklefs and Schluter, 1993; Fleagle and Reed, 1999; Webb et al., 2002; Graham et al., 2006). This is surprising because many studies have shown that historical factors such as dispersal, vicariance, and extinction are critical for understanding species distributions (Cracraft, 1994; Frost et al., 2003; Wiens and Donoghue, 2004) and consequently the composition of communities.

Some recent examinations of historical effects on communities have centered on relating the geographic distance between communities to their species richness and/or taxonomic similarity (Ganzhorn, 1998; Condit et al., 2002; Legendre et al., 2005; Lehman, 2006).

Accounting for geographic distance between communities is critical from both a statistical and biological perspective (Legendre et al., 2005). Environmental and community composition data are often spatially autocorrelated, which may inflate the degrees of freedom in standard statistical analyses (Borcard et al., 1992). In addition, geographic effects may be the result of historical factors such as dispersal, vicariance, and extinction (Atmar and Patterson, 1993; Wright and Jernvall, 1999). The colonization of populations into new areas results in geographic range expansion and/ or eventual speciation. Therefore, communities in close spatial proximity exhibit similar species compositions, and this similarity decreases with geographic distance because of differences in the ability of species to disperse long distances (Ganzhorn, 1998; Legendre et al., 2005). Conversely, vicariance events would result in reducing the geographic ranges of taxa due to speciation, resulting in sister taxa inhabiting communities in close proximity to each other. Similarly, local and complete extinction of species would reduce the distribution of species and remove them from communities (Atmar and Patterson, 1993; Godfrey et al., 1997; Struhsaker, 1999; Wright and Jernvall, 1999).

Few studies have tested hypotheses examining the potential impact of geography on the taxonomic structure of primate communities. Two studies that have investigated this topic relate the geographic distance between communities to their similarity in taxonomic composition. In western Madagascar, Ganzhorn (1998) found that communities in close geographic proximity were similarly composed taxonomically, and this similarity decreased as geographic distance increased. A study by Lehman (2006) found a similar pattern in primate communities in Guyana. Both authors attribute these patterns to differences in the colonization ability of species over evolutionary time.

A body of evidence from non-primate taxa shows that both ecological and historical processes play significant roles in affecting community structure at local and broader scales (e.g., Graham et al., 2005); yet, we currently have little knowledge of the relative importance of these influences for primate communities (Reed and Bidner, 2004). Therefore, the goals of this study were 1) to identify the relative importance of environmental characteristics and historical factors (using the geographic distance between communities as a proxy for history) for predicting the variation in species composition across sites (i.e. beta diversity as defined by Whittaker 1960, 1972), and 2) how do these effects differ across regions. As demonstrated by previous studies, a relationship between geographic distance and the taxonomic similarity of communities may be interpreted as the result of historical processes, especially species dispersal and vicariance (Ganzhorn, 1998; Legendre et al., 2005; Lehman, 2006). The first goal essentially tests the three major hypotheses for the origin of beta diversity as presented by Legendre et al. (2005): 1) species composition does not change across a region, 2) species composition varies in an autocorrelated fashion, and 3) species composition is related to environmental characteristics, with hypotheses 2 and 3 not being mutually exclusive. Hypothesis 1 acts as a null model, and is supported if no predictor variables are related to variation in species composition, (i.e. species are randomly distributed within a region). Hypothesis 2 is related to the idea that species are ecologically interchangeable (i.e. flexible), and their distributions are primarily dependent on historical patterns of dispersal and/or vicariance (Hubbell, 2001). Hypothesis 3 stresses the importance of habitat characteristics for species persistence, with species being adapted to certain ecological niches that are only available in particular environments (Hutchinson, 1957). Primates provide an ideal group for examining this issue because they are well studied in a myriad of habitats across several continents and their presence/absence at a location can be assigned confidently.

METHODS
Datasets

Data for 168 primate communities from Africa (Fig. 1a, $n = 47$), Madagascar (Fig. 1b, $n = 33$), the Neotropics (i.e., Central and South America) (Fig. 1c, $n = 45$), and Asia (Fig. 1d, $n = 43$) were accumulated from the literature (Supporting Information Appendix 1). For each region, information was gathered from established study sites, with three datasets being created: 1) geographic location of each study site (i.e. latitude and longitude); 2) environmental characteristics of the site including: a) mean annual rainfall, b) rain seasonality, c) mean altitude, d) mean minimum monthly temperature, and e) mean maximum monthly temperature; and 3) the presence/absence of primate species at each study site (i.e. the primate community). A total of 200 primate species were included in this study.

Although many communities have accurate information regarding the species present at the site, it is unlikely that this is absolutely true for all communities. Detecting nocturnal and/or cryptic species is often challenging, and may result in false absences at some sites. In addition, although the geographic breadth of the study is large, it is not exhaustive. There may be areas of endemism (and their associated species) within each region that are not represented in the study. Considering the number of taxa and communities included in the analyses, these factors are unlikely to have a significant impact on the results.

Ideally, detailed information regarding the habitat characteristics of each community would be available. Unfortunately, these data are not available for most study sites. Instead, researchers examining macroecological questions have successfully utilized abiotic variables as proxies for habitat characteristics (Reed and Fleagle, 1995; Graham et al., 2005; van Schaik et al., 2005).

In many instances, the environmental characteristics of a site were not presented by previous researchers. In these cases, data were obtained from the WorldClim climate database (Hijmans et al., 2005). This database contains several geo-referenced climate data layers based on thousands of long-term weather stations from across the globe. The environmental values in this database were extracted for the geographic location of each community using the "extract by point" function in ArcGIS 9.0. Rain seasonality was defined as the mean vector of rain across months, using the circular statistic, "r" (Batschelet, 1981). This measure was calculated using the circular statistics software Oriana 2.0.

The species taxonomy was based on: Jolly (1993) for baboons, Oates et al. (1994) for African colobine monkeys, Brandon-Jones (1996) for Asian colobine monkeys, Fleagle (1999) for macaques and African catarrhines (except baboons), Grubb et al. (2003) for African prosimians, Goodman and Benstead (2003) for Malagasy primates, and Groves (2001) for the remaining taxa.

Data analyses

For each region, a canonical correspondence analysis (CCA) (Borcard et al., 1992; Duivenvoorden et al., 2002; Legendre et al., 2005) was implemented to examine the relative importance of environmental and geographic variables on community composition. This analysis is commonly used in recent studies of beta diversity (e.g.
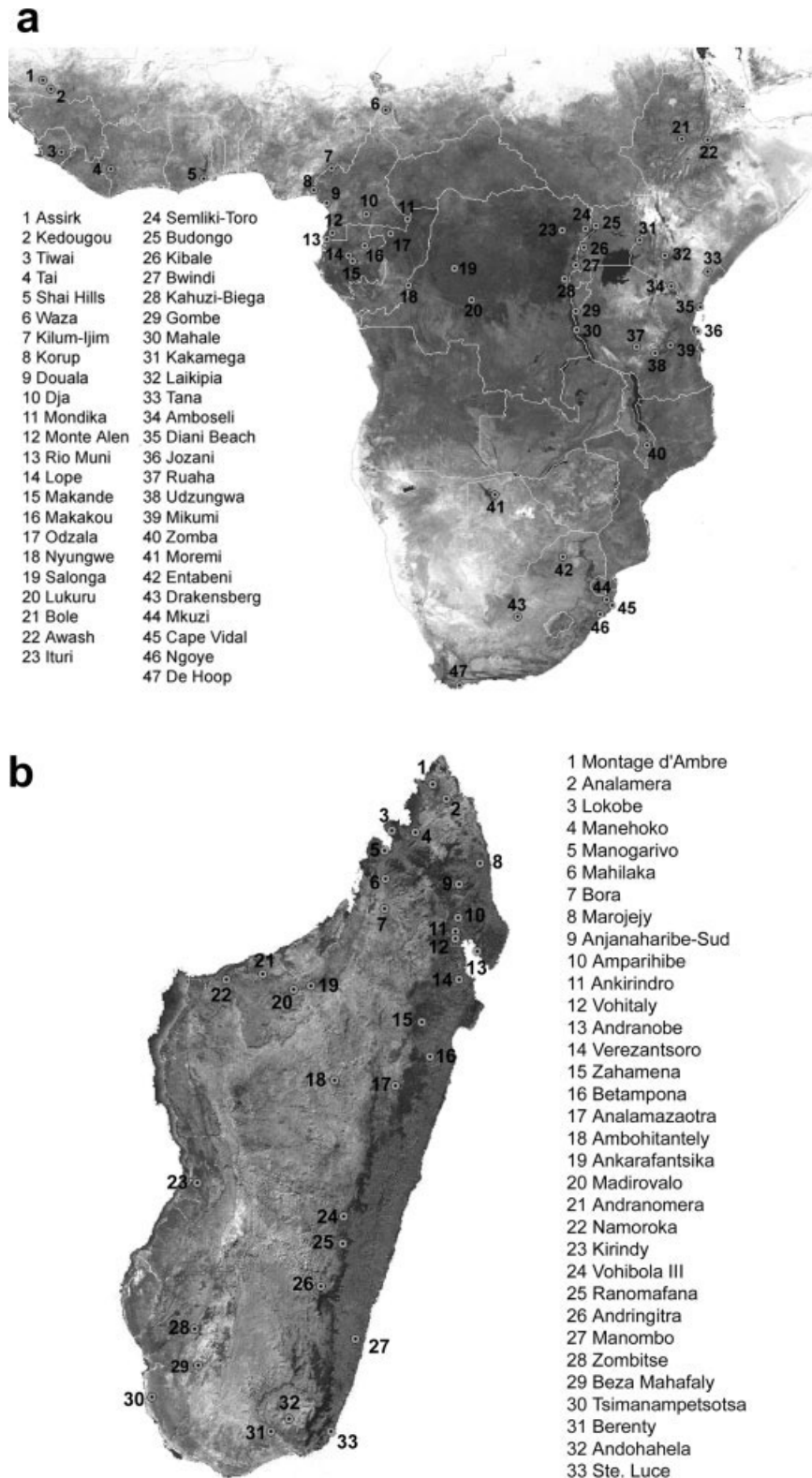
1 Assirk
2 Kedougou
3 Tiwai
4 Tai
5 Shai Hills
6 Waza
7 Kilum-Ijim
8 Korup
9 Douala
10 Dja
11 Mondika
12 Monte Alen
13 Rio Muni
14 Lope
15 Makande
16 Makakou
17 Odzala
18 Nyungwe
19 Salonga
20 Lukuru
21 Bole
22 Awash
23 Ituri
24 Semliki-Toro
25 Budongo
26 Kibale
27 Bwindi
28 Kahuzi-Biega
29 Gombe
30 Mahale
31 Kakamega
32 Laikipia
33 Tana
34 Amboseli
35 Diani Beach
36 Jozani
37 Ruaha
38 Udzungwa
39 Mikumi
40 Zomba
41 Moremi
42 Entabeni
43 Drakensberg
44 Mkuzi
45 Cape Vidal
46 Ngoye
47 De Hoop

1 Montage d'Ambre
2 Analamera
3 Lokobe
4 Manehoko
5 Manogarivo
6 Mahilaka
7 Bora
8 Marojejy
9 Anjanaharibe-Sud
10 Amparihibe
11 Ankirindro
12 Vohitaly
13 Andranobe
14 Verezantsoro
15 Zahamena
16 Betampona
17 Analamazaotra
18 Ambohitantely
19 Ankarafantsika
20 Madirovalo
21 Andranomera
22 Namoroka
23 Kirindy
24 Vohibola III
25 Ranomafana
26 Andringitra
27 Manombo
28 Zombitse
29 Beza Mahafaly
30 Tsimanampetsotsa
31 Berenty
32 Andohahela
33 Ste. Luce

Fig. 1. Communities included in the study are from: **a**) Africa, **b**) Madagascar, **c**) the Neotropics, and **d**) Asia.

c

34 El Triunfo
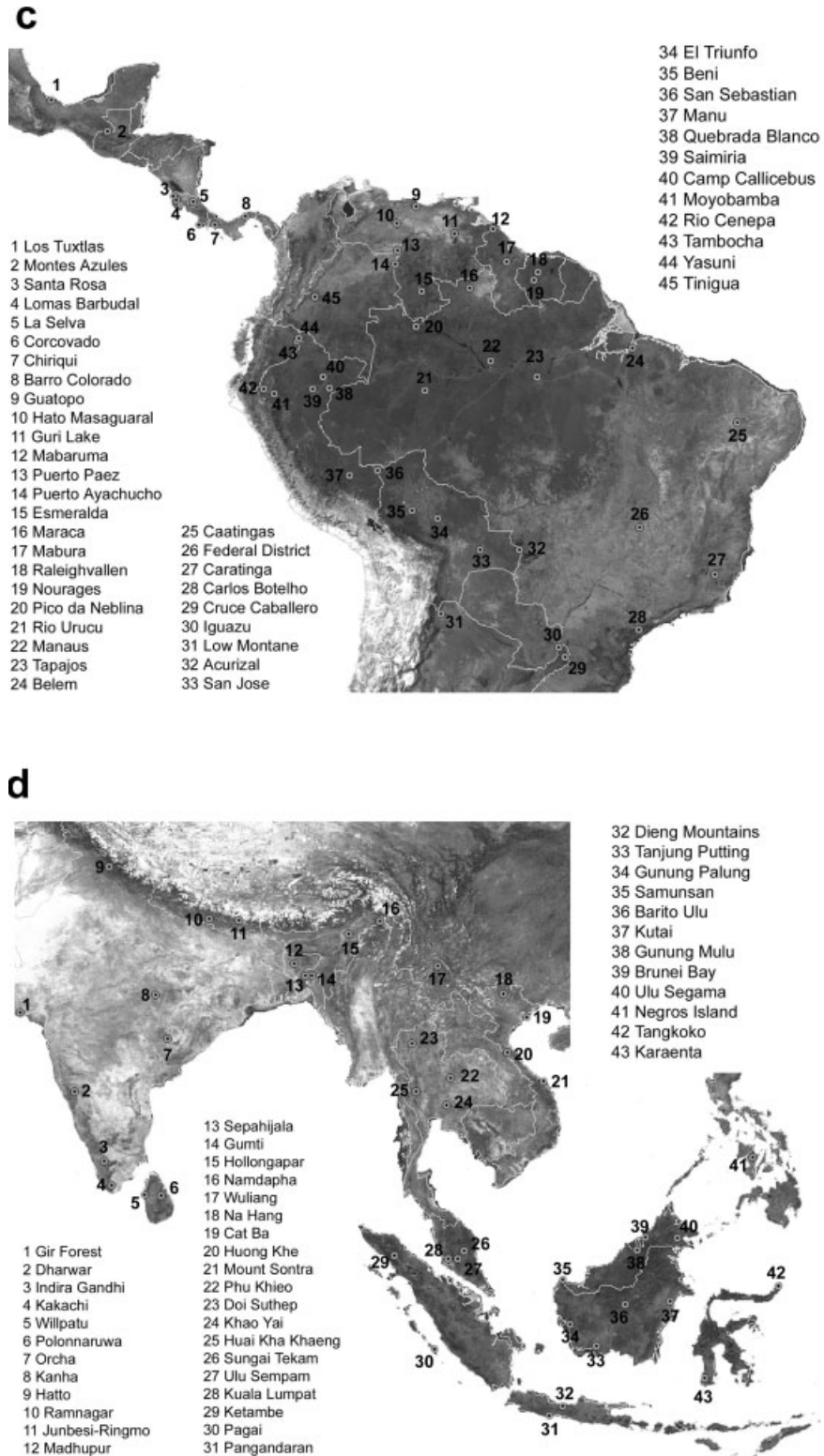35 Beni
36 San Sebastian
37 Manu
38 Quebrada Blanco
39 Saimiria
40 Camp Callicebus
41 Moyobamba
42 Rio Cenepa
43 Tambocha
44 Yasuni
45 Tinigua

1 Los Tuxtlas
2 Montes Azules
3 Santa Rosa
4 Lomas Barbudal
5 La Selva
6 Corcovado
7 Chiriqui
8 Barro Colorado
9 Guatopo
10 Hato Masaguaral
11 Guri Lake
12 Mabaruma
13 Puerto Paez
14 Puerto Ayachucho
15 Esmeralda
16 Maraca   25 Caatingas
17 Mabura   26 Federal District
18 Raleighvallen   27 Caratinga
19 Nourages   28 Carlos Botelho
20 Pico da Neblina   29 Cruce Caballero
21 Rio Urucu   30 Iguazu
22 Manaus   31 Low Montane
23 Tapajos   32 Acurizal
24 Belem   33 San Jose

d

32 Dieng Mountains
33 Tanjung Putting
34 Gunung Palung
35 Samunsan
36 Barito Ulu
37 Kutai
38 Gunung Mulu
39 Brunei Bay
40 Ulu Segama
41 Negros Island
42 Tangkoko
43 Karaenta

                      13 Sepahijala
                      14 Gumti
                      15 Hollongapar
                      16 Namdapha
                      17 Wuliang
                      18 Na Hang
                      19 Cat Ba
1 Gir Forest   20 Huong Khe
2 Dharwar   21 Mount Sontra
3 Indira Gandhi   22 Phu Khieo
4 Kakachi   23 Doi Suthep
5 Willpatu   24 Khao Yai
6 Polonnaruwa   25 Huai Kha Khaeng
7 Orcha   26 Sungai Tekam
8 Kanha   27 Ulu Sempam
9 Hatto   28 Kuala Lumpat
10 Ramnagar   29 Ketambe
11 Junbesi-Ringmo   30 Pagai
12 Madhupur   31 Pangandaran

Fig. 1. Continued.

Cleary and Genner, 2006; Heino and Muotka, 2006) and is advantageous because it accounts for potential covariation among both predictor variables (i.e., environmental and geographic distance effects) and dependent variables (i.e., the presence or absence of species).

Traditionally, studies examining the predictors of beta diversity have used partial Mantel tests (e.g. Parris and McCarthy, 1999; Spencer et al., 2002). Predictor variables were transformed into dissimilarity/distance matrices (e.g. environmental dissimilarity, geographic dis-

tance, dissimilarity in species composition), and then used in partial Mantel tests. Instead of using distance matrices, a canonical analysis using the raw data can be utilized to answer the same question. Canonical analyses are preferred because they have greater statistical power due to their use of the raw data, as opposed to distance matrices (Legendre, 2000; Legendre et al., 2005). In addition, canonical analyses provide detailed information in numeric and visual form (through biplots) about the relationships between each predictor variable and the presence/absence of species. These results are not available through Mantel tests.

CCA was also used as a variance partitioning method. This method calculates the degree of variation in community composition explained by environmental effects independent of space, geographic distance effects independent of environmental characteristics, and spatially correlated environmental variables. Several steps were needed for this procedure: 1) all environmental and spatial variables were used to predict community composition to obtain the total variance explained by all variables (V_t), 2) only the environmental variables were used to predict community composition (V_e), 3) only latitude and longitude were used to predict community composition (V_s), 4) the independent effects of environment were

then calculated as $V_{ie} = V_t - V_s$, 5) the independent effects of geographic distance were calculated as $V_{is} = V_t - V_e$, and 6) the spatially correlated environmental effects were calculated as $V_{se} = V_s + V_e - V_t$.

Following previous studies (Cleary and Genner, 2006; Heino and Muotka, 2006), the predictor variables were entered into the model in a forward stepwise fashion with an alpha level of 0.05. This procedure reduces the possible effects of multicolinearity among the predictor variables, which artificially increase the explained variance (Tabachnick and Fidell, 1989). Only statistically significant variables were used in subsequent CCA. Statistical significance was calculated by a permutation approach utilizing 9,999 iterations. All CCA were conducted with CANOCO (ter Braak and Smilauer, 2002).

Following Reed and Bidner (2004), a hierarchical cluster analysis using the unweighted pair-group method with arithmetic mean (UPGMA) (McGarigal et al., 2000) based on a Dice (Sørensen) similarity index (Magurran, 1988) was used to examine the taxonomic similarity of primate communities in each region. The Dice similarity index is defined as: $D = 2_j/(2_j + a + b)$, where j is the number of species in common at both sites, a is the number of species at site A, and b is the number of species at site B.

In addition to using species, this technique also incorporates the presence or absence of higher (e.g., genus, subfamily, etc.) and lower (e.g., subspecies) taxonomic groups (Porzecanski and Cracraft, 2005). Cracraft (1991) argued that historical signals in biogeography could be recovered when hierarchical taxonomic information is utilized, especially when taxonomy reflects phylogeny. This is generally the case for primates, though this method does not account for the divergence times among taxa. The dendrograms generated from the analyses were presented for visualizing the community relationships. All cluster analyses were conducted with SPSS 13.0.

RESULTS

Both geographic and climatic variables explained statistically significant amounts of variation in community structure; yet, the total amount of explained variation differed across regions (range, from 17.5 to 33.1%). In addition, the variance partitioning yielded important differences across regions (see Fig. 2). Purely spatial effects explained a statistically significant amount of variation in primate communities across all regions, with the most variation in Asian communities and the least variation
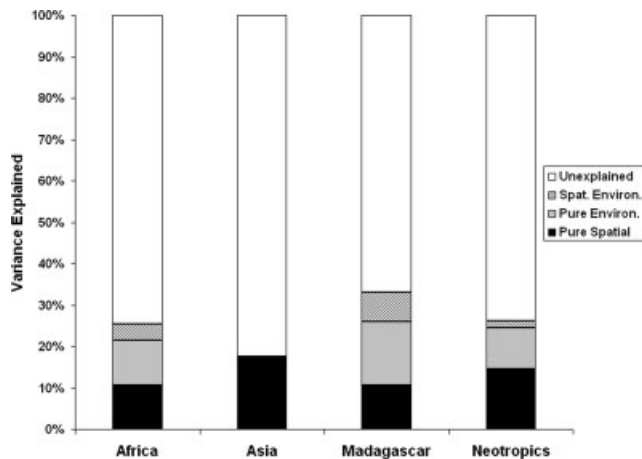

Fig. 2. Graphical representation of the amount of variance in the taxonomic structure of primate communities explained by: 1) spatially structured environmental effects, 2) pure spatial effects (i.e. geographic distance), and 3) pure environmental effects. The amount of variance unexplained by space and environment is also indicated.

TABLE 1. *Significance of predictor variables for explaining the taxonomic structure of primate communities*[a,b]

Predictor variables	Africa		Asia		Madagascar		Neotropics	
	F ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value
Latitude	*2.47*	*<0.003*	*3.64*	*<0.001*	0.90	0.557	*4.10*	*<0.001*
Longitude	*3.14*	*<0.001*	*4.55*	*<0.001*	*6.74*	*<0.001*	*3.73*	*<0.001*
Annual rain	*5.15*	*<0.001*	0.81	0.659	1.08	0.364	0.79	0.759
Rain seasonality	*2.66*	*<0.002*	1.23	0.211	*2.13*	*0.011*	*2.78*	*<0.001*
Mean min. temp.	1.13	0.291	0.51	0.952	0.99	0.443	1.02	0.433
Mean max. temp.	0.71	0.780	0.71	0.766	*4.29*	*<0.001*	*2.51*	*<0.001*
Altitude	1.22	0.228	0.62	0.844	0.98	0.446	1.36	0.102

[a] Number of primate communities in each region: Africa = 47, Asia = 43, Madagascar = 33, Neotropics = 45.
[b] Variables were entered into the model in a forward stepwise fashion using Monte Carlo tests with 9,999 permutations to assess statistical significance. Only variables with a *P* value below 0.05 were entered into the full model. The *F* ratio and *P* values of these variables are denoted by italics.
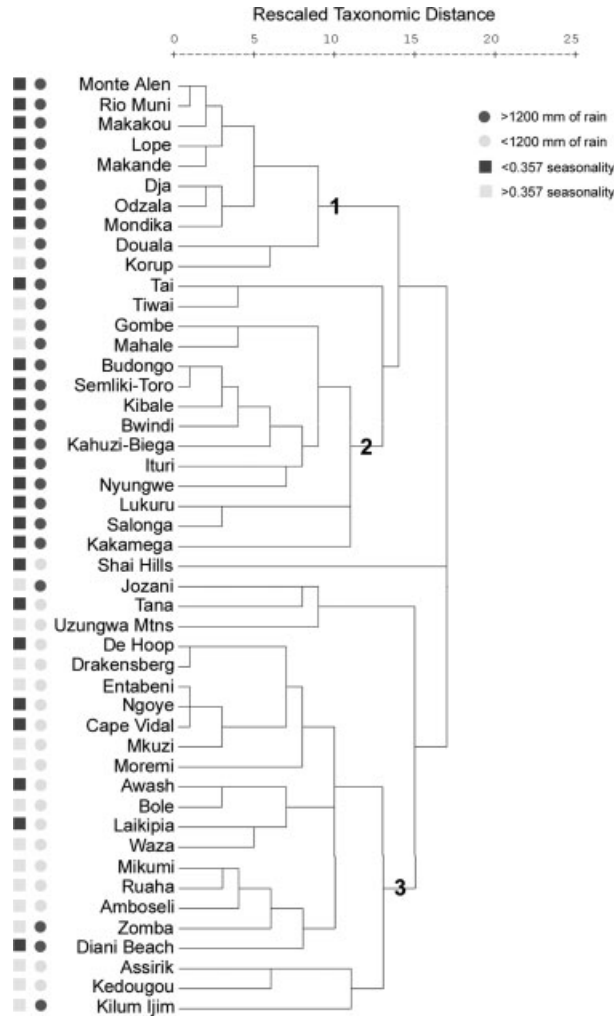
Fig. 3. Dendrogram of the UPGMA cluster analysis of the taxonomic distance of African primate communities. The first cluster is comprised of communities from Central Africa. The second cluster contains communities from East Africa. The third cluster consists of sites with relatively low levels of rainfall and high levels of rain seasonality. Communities from southern and eastern Africa dominate this group; yet, many other sites do not form easily discernable groups based on geography. Many of these remaining communities do not cluster geographically, yet share relatively low levels of rain. Low and high rainfall sites are defined as being below or above the mean annual rainfall for all sites in Africa (1,415 mm rain per year). High and low rain seasonality sites are defined as being below or above the mean vector of rainfall of 0.357.
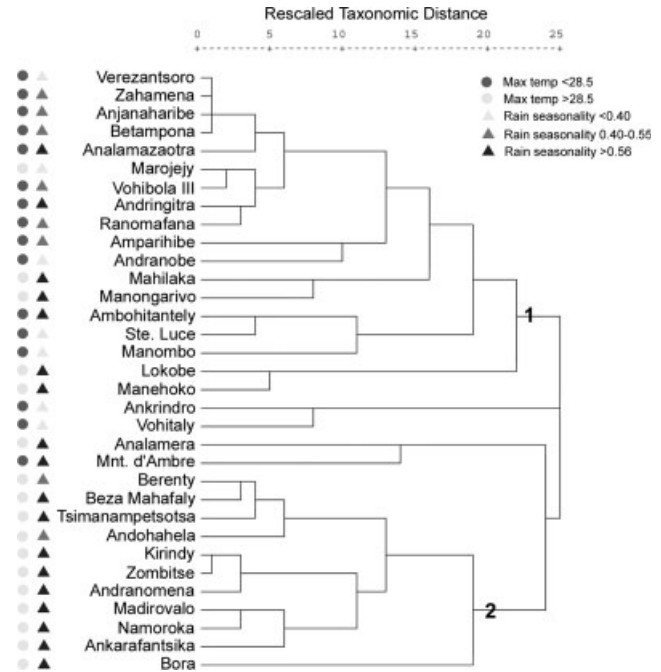

Fig. 4. Dendrogram of the UPGMA cluster analysis of the taxonomic distance of Malagasy primate communities. The first group contains communities from eastern Madagascar and the Sambirano area. The second cluster consists of all of the sites from west and southern Madagascar. In addition to geographic clustering, environmental differences characterize these areas. Sites are defined as being below or above the average maximum mean monthly temperature for all sites in Madagascar (28.5°C). Similarly, sites are separated into three rain seasonality classes based on the average rain seasonality of sites (0.56), and one and two standard deviations below the average value (0.40–0.55 and <0.40, respectively).

in Africa and Madagascar. In contrast, purely environmental effects were important in three of the four regions. It did not account for any of the variation in Asian communities and explained the most variation in Malagasy communities. Similarly, spatially structured environmental characteristics explained no community structure variation in Asia, yet were most important for the primate communities of Madagascar (Table 1).

The importance of geographic distance for predicting the taxonomic structure of primate communities independent of environmental characteristics is emphasized by latitude and longitude being statistically significant predictors of community structure. Both of these variables are important in each region, except for Madagas-

car. In Madagascar, only longitude is a significant geographic predictor variable.

Two variables were not chosen as predictor variables in all regions: mean minimum temperature and altitude. Mean annual rainfall was an important predictor of community composition only in Africa. Mean maximum temperature was entered into the full model to explain community structure in Madagascar and the Neotropics. Finally, rain seasonality was the most important environmental variable explaining the taxonomic structure of primate communities, being a significant predictor in all regions except for Asia (Table 1). A visual depiction of the relationship between predictor variables and the occurrence of particular species is found in Supporting Information Appendix 2.

In several respects, the UPGMA cluster analyses supported the CCA results. In general, the primate communities group into geographic clusters in each region, reflecting the importance of geographic distance in structuring communities (Figs. 3–6). In addition, in every region except for Asia, some community clusters are associated not with geographic location, but with similarity in environmental characteristics.

DISCUSSION

The results of this study demonstrate an effect of both evolutionary history (as measured by geographic distance) and environmental factors on primate beta diver-
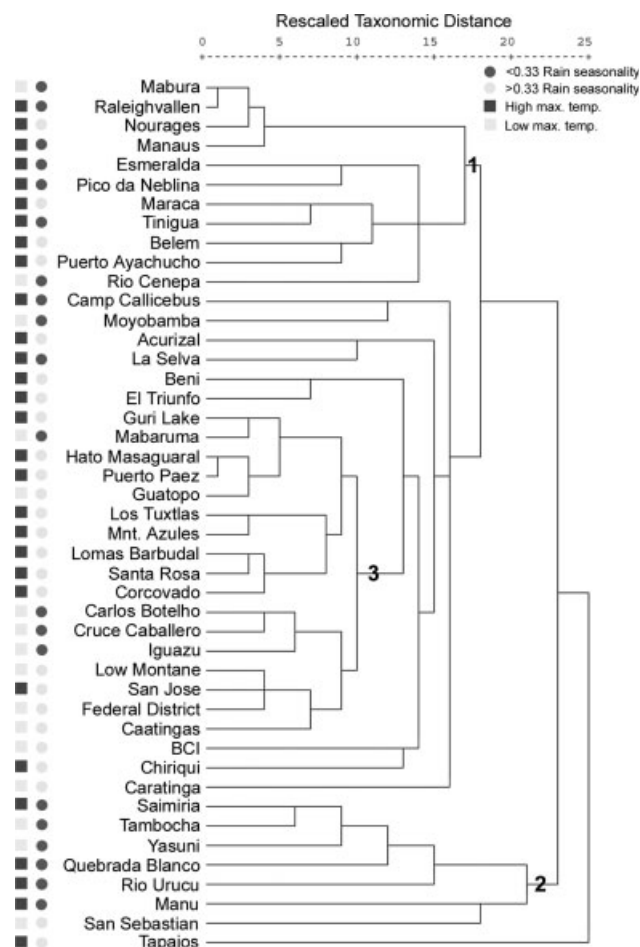
Fig. 5. Dendrogram of the UPGMA cluster analysis of the taxonomic distance of Neotropical primate communities. Three major clusters were found in the Neotropics, the first containing sites from the Guyana Shield, a second comprised mostly of communities from western Amazonia, and a third consisting of many of the remaining communities. The communities in this third cluster are geographically dispersed; yet, many exhibit high degrees of rain seasonality. In addition, one group of communities within this cluster exhibits high maximum monthly temperatures, whereas the other group contains communities with low temperatures. Low and high rain seasonality sites are defined as being below and above the average rain seasonality of sites in the Neotropics (0.33).

Fig. 6. Dendrogram of the UPGMA cluster analysis of the taxonomic distance of Asian primate communities. The first cluster consisted of all the Bornean communities. The second cluster comprised sites from Thailand and peninsula Malaysia. The third cluster contained the communities from India, Sri Lanka, China, Vietnam, Sulawesi, Philippines, and Java. The relatively small number of primates found in the communities of this third major cluster is probably an important factor for the clustering of these geographically dispersed areas.

sity. Geographic variables were important predictors of community structure in all regions. The independent effect of geography demonstrates that many species are ecologically flexible, with their absence or presence in a community being not dependent on particular environmental conditions, but due to their evolutionary history. Recent studies have also found evidence for the importance of evolutionary factors for explaining macroecological patterns. Several researchers have found that historical processes are important predictors of bird (Hawkins et al., 2005; Thomas et al., 2008), bat (Stevens, 2006), and frog (Wiens et al., 2006) species richness. In general, we have little knowledge if the factors influencing species richness patterns are the same as those affecting patterns of community composition. For primates, preliminary results suggest that contemporary climate patterns are better predictors of species richness than of
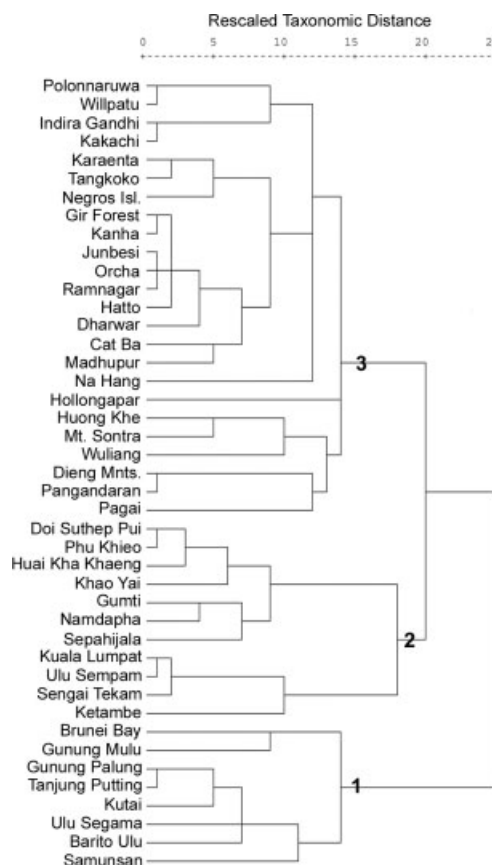
community composition (Marshack and Kamilar, submitted for publication).

In addition to geography, climatic factors are important predictors of variation in species composition in all regions except Asia. Rain seasonality was the most consistently important environmental variable affecting the species composition of communities. This may be related to the inability of some species to persist in seasonal habitats that exhibit large fluctuations in food availability (Foster, 1982). Interestingly, the maximum temperature at a site was only an important factor influencing community structure in Madagascar and the Neotropics. Communities in Madagascar and the Neotropics contain a relatively large proportion of small-bodied species and display less body mass variation compared with African and Asian communities (Ganzhorn, 1999). The relationship between temperature and community structure may be a result of higher energetic costs of thermoregulation for small animals, especially Malagasy primates (Lahann et al., 2006).

It is important to note that the variables incorporated into these analyses are not exhaustive, and other factors such as anthropogenic impacts, inter-annual climatic variation, and interspecific competition also may affect

community composition (Connell, 1983; Struhsaker, 1999; Harrison, 2001). These unaccounted factors are likely the reason for rather high levels of unexplained variation commonly observed in broad-scale studies of beta diversity. That being said, the amount of unexplained variation in this study is similar to previous examinations of beta diversity. Heino and Muotka (2006) explained 53% of snail and 48% of clam community assemblage variation across 22 lakes throughout Finland. Cleary and Genner (2006) examined butterfly communities in nine regions of Borneo, and the amount of explained variation in community structure ranged from 6 to 70%, with a mean of 24%. Although these aforementioned studies explained similar levels of variation to this study, they examined community variation across a much smaller spatial scale and included fewer species.

Geography and the taxonomic structure of primate communities

Compared to environmentally focused studies, research examining historical effects on primate communities is relatively sparse (but see Ganzhorn, 1998; Fleagle and Reed, 1999; Lawes and Eeley, 2000; Lehman, 2006). Fleagle and Reed (1996) showed that primate communities on the same continent occupied a similar ecospace, and were distinct from communities in other regions. A complementary study found a positive relationship between phylogenetic distance and ecological dissimilarity (measured along several niche axes) of primate species within communities (Fleagle and Reed, 1999); yet, regions exhibited differences in the strength of association. This relationship was weaker in the Neotropics and Madagascar because these regions contain several lineages that diverged in a relatively short time frame; yet, the resulting taxa have relatively high ecological diversity (Fleagle and Reed, 1999).

Additional studies used an alternative approach to address this issue, using geographic distance as a proxy for historical processes. How do historical processes result in community similarity being correlated to geographic distance? One possibility may be related to the correlation between ecological specialization and geographic range size (Harcourt et al., 2005). Two hypothetical scenarios would not display a relationship between geographic distance and community similarity. First, if all species were found in all communities, there would be no variation in community composition. Second, if species were specialized to the point of only being present in a single community, then there would be no similarity in species composition among any communities. In reality, most communities contain a combination of generalist and specialist species. Therefore, the differential dispersal ability and/or rate of vicariance among taxa likely produce the negative relationship between geographic distance and similarity in community composition. Ganzhorn (1998) and Lehman (2006) argued a similar scenario, yet focused only on dispersal, to explain the geographic distance effect in lemur communities of western Malagasy forests and Guyana, respectively. Either the variation in dispersal ability or speciation rate (which are often inversely related) among taxa may lead to a geographic distance effect explaining the taxonomic structure of primate communities. There are several examples of this in each region.

In Africa, the contraction and expansion of forests throughout the last 20 million years may have played a pivotal role in leading to the diversification of several African lineages, most notably, the *Cercopithecus* monkeys (Hamilton, 1988). Most species have relatively small geographic ranges, with several species being ecological replacements (Chapman et al., 2002). In contrast is the broad geographic range and ecological flexibility of baboons (*Papio hamadryas*) and vervet monkeys (*Chlorocebus aethiops*) (Jolly, 1993; Butynski, 2002; Kamilar, 2006). The increased dispersal ability of these taxa has resulted in geographic barriers playing a lesser role in the speciation process, as evidenced by the continued gene flow among populations (Rogers, 2000). Although geographic variants exist, most authorities agree that complete speciation has not occurred (Jolly, 1993; Frost et al., 2003; Bohm and Mayhew, 2005). Therefore, one can view the good dispersal ability of baboons and vervet monkeys as a mechanism that maintains species cohesion, and conversely reduces diversification at the full species level.

In Madagascar, two scales of geographic barriers are evident and play an important role in shaping communities. For many primate species, the major geographic barrier in Madagascar is the Central Plateau. The results of this study and previous examinations of the faunal distribution of Madagascar support an east-west biogeographic division. Yet, recent evidence suggests that dispersal of species between eastern and western Madagascar across this barrier has likely occurred in several lineages (Goodman and Ganzhorn, 2004; Yoder and Heckman, 2006). On a smaller spatial scale, several rivers are known to bind the geographic ranges of some taxa and not others (Lehman and Wright, 2000; Goodman and Ganzhorn, 2004).

In the Neotropics, most communities comprise both specialist and generalist taxa (as defined by geographic range size) (Peres and Janson, 1999). The relatively high species diversity in genera such as *Callicebus* and *Saguinus* is probably related to allopatric speciation caused by riverine geographic barriers found throughout the Amazon Basin (Ayres and Clutton-Brock, 1992; but see Gascon et al., 2000). The relatively high degree of allopatric speciation in these clades is in contrast to other larger bodied platyrrhine species (e.g., *Cebus* and *Alouatta*) that have a better dispersal ability across these barriers (Ayres and Clutton-Brock, 1992; Lehman, 2004). Consequently, Neotropical primate communities generally consist of at least one *Cebus* and *Alouatta* species, complemented by additional species that tend to have smaller geographic ranges.

Finally, in Asia, the primary geological phenomenon driving the correlation between geographic distance and community structure may be the rise and fall of sea levels and its effect on the land masses of the Sunda Shelf (Rohling et al., 1998). The changing degree of connectivity among these land masses provided numerous opportunities for the dispersal, speciation, and/or extinction of primates throughout these areas (Harrison et al., 2006).

In addition to the Sunda Shelf, several rivers and mountain ranges provide opportunities for limiting dispersal to some species and not others (Meijaard and Groves, 2006). What is especially important is how these geographic events translated into the evolutionary history of Asian primates. This can be illustrated by the almost omnipresent occurrence of species such as *Macaca mulatta* and *Macaca nemistrina* in combination with relatively high turnover of gibbon and colobine species, especially on the Sunda Shelf.

Environmental factors and the taxonomic structure of primate communities

Although primate species richness is related to mean annual rainfall (Reed and Fleagle, 1995; Kay et al., 1997), the importance of this variable in predicting the taxonomic similarity of primate communities is limited. This is interesting because the number of species in a community may also be related to the taxonomic similarity among communities. If two communities display a disparate number of species, then by default they are limited in the degree of taxonomic similarity.

The only region where mean annual rainfall was an independent correlate of community structure was Africa. This pattern is due to communities that are widely separated, experience dry environmental conditions, and contain a similar composition of primates, namely baboons, vervet monkeys, and galago species. Africa is the only continent on which this situation occurs. Rain seasonality is the other climatic variable affecting African primate communities, and is, as expected, negatively correlated with mean annual rainfall. Environmentally stable communities (e.g., those with low rain seasonality and high rainfall) contain more species. In addition, the species associated with these habitats include *Cercopithecus mona*, *Colobus satanas*, and *Cercocebus torquatus*. Although *Colobus satanas* is a specialized folivore, it is the most frugivorous African colobine species (McKey et al., 1981). The presence of this species in more stable habitats may be related to more consistent levels of fruit availability at these sites.

In Madagascar, two climatic variables were significantly correlated with primate community similarity: rain seasonality and maximum temperature. The eastern portion of Madagascar is subjected to more consistent rainfall and lower maximum temperatures, with the opposite true in the west and south (Jury, 2003). The degree of rain seasonality in Madagascar tends to be inversely related to species richness, which may have some effect on community taxonomic structure. In the eastern portion of Madagascar, primate communities are larger and many of them contain species that are restricted to the eastern forests (Ganzhorn et al., 1999). These endemic taxa, including *Indri*, *Varecia*, and *Avahi*, are all dietary specialists. Both *Indri* and *Avahi* are amongst the most folivorous of all primates, with over 75 and 90% of their diet consisting of leaves, respectively (Ganzhorn et al., 1985; Britt et al., 2002). In addition, *Varecia* is perhaps the most frugivorous Malagasy lemur, with over 80% of its diet consisting of fruit (Vasey, 1997). The more consistent availability of food resources in the less seasonal habitats of Madagascar's eastern evergreen forests may be an important influence on the presence of these taxa. In addition to rainfall patterns, maximum temperature plays an important role in structuring Malagasy communities, perhaps acting as a body-mass filter. For instance, many of Madagascar's smallest primates, the cheirogalieds, are often found in sites with high maximum temperatures. In particular, the presence of *Microcebus myoxinus*, *M. murinus*, and *Mirza coquereli* is correlated with high maximum temperatures. High maximum temperatures may reduce costs of thermoregulation in these small-bodied taxa (Lahann et al., 2006).

In the Neotropics, community structure was related to rain seasonality and maximum temperature. Many areas of the Neotropics that experience a relatively high degree of rain seasonality exhibit small primate communities, usually consisting of *Cebus, Alouatta,* and *Ateles*. The sites exhibiting these types of communities are geographically dispersed, with sites in Mexico (without *Cebus*), the dry forests of Costa Rica, parts of Venezuela, and eastern Brazil. The occurrence of *Alouatta* and *Cebus* species in almost all communities, especially those in species-poor habitats may be related to the ecologically flexible characteristics of these taxa. *Alouatta* is able to consume a large amount of leaves, which are typically more abundant in seasonal habitats; yet, they also use fruits as a major dietary resource (Estrada and Coates-Estrada, 1984). Many *Cebus* populations are known to shift dietary resources during seasonal changes throughout the year and also show interpopulation variation (Janson and Boinski, 1992). Some capuchin species can also access food resources unavailable to other primates via tool use (Fragaszy et al., 2004).

Neotropical communities in stable environments often contain species that are not present in seasonal habitats. For example, *Pithecia pithecia, Ateles paniscus,* and *Chiropotes satanas* are largely distributed throughout the Guyana Shield, which generally displays low levels of rain seasonality. These species exhibit extreme dietary specialization, with fruit and seeds consisting of about 90% of the diet in *P. pithecia* (Norconk and Conklin-Brittain, 2004), 80% in *A. paniscus* (van Roosmalen, 1985), and over 90% in *C. satana*s (van Roosmalen et al., 1981).The consistent availability of food in these stable habitats may be a requirement for maintaining viable populations for these dietary specialists. These results suggest that environmental stability and dietary specialization are connected because of the more consistent availability of fruit in these habitats. Further investigations of this scenario are warranted because of some contrasting findings from van Schaik and Pfannes (2005).

In more seasonal environments, plant productivity is reduced and/or less stable, limiting the potential dietary resources in the environment (Mitchell and Csillag, 2001). These resource troughs may result in higher mortality (Foster, 1982) and/or reduced reproductive output (Gould et al., 1999) for diet-specialized species. Therefore, seasonal effects may filter out species that cannot persist during lean periods in these habitats. Interestingly, a recent study by van Schaik et al. (2005) did not find a strong relationship between seasonality and species richness.

No climatic variables were significantly related to primate community structure in Asia. There may be several reasons for this lack of relationship. First, many communities throughout the Sunda Shelf and southeast Asia islands have relatively uniform environmental conditions yet also display a high turnover of species. Throughout this region, *Presbytis* and gibbon species diversity is high, with communities exhibiting similar environmental conditions. Another reason may be related to the mast fruiting seasons present in many areas of Asia (Sakai, 2002). The large-scale production of fruit and flowers in multi-year intervals may be an important influence of community taxonomic structure, yet may not be highly correlated to the environmental variables used in this study.

CONCLUSIONS

This study simultaneously examined the effects of environmental and geographic factors on the taxonomic composition of 168 primate communities across the four major regions where they are found. Two types of multi-

variate analyses showed that both environmental factors and geographic distance were significant predictors of primate community composition; yet, the relative importance of these effects varied across regions. Geographic distance between communities predicted community composition independent of abiotic factors in each region. This effect may be the result of historical processes such as species dispersal and/or vicariance. In addition, this demonstrates the ecological flexibility of many primate species, where communities in close proximity to each other are taxonomically similar even if their habitat characteristics differ.

The role of environmental factors on the composition of primate communities is more complex. Different abiotic factors are important for predicting the taxonomic structure of primate communities in different regions, and no broad scale environmental factors are significant predictors of Asian communities. The effects of climatic factors demonstrate that ecological filtering influences the presence or absence of many species, independent of their evolutionary history.

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