

Species Co-Occurrence Patterns and Dietary Resource Competition in Primates

Jason M. Kamilar^{1,2*} and Justin A. Ledogar³

¹Department of Anthropology, Yale University, New Haven, CT 06520-8277

²Molecular Anthropology Laboratory, Yale University, New Haven, CT 06520-8277

³Department of Anthropology, University at Albany, Albany, NY 12222

KEY WORDS assembly rules; species distribution; null model analysis; guild structure; community ecology

ABSTRACT Diamond (Assembly of species communities. In: Cody ML, Diamond JM, editors. Ecology and evolution of communities. Cambridge: Belknap. p 342–444 (1975)) argued that interspecific competition between species occupying similar niches results in a nonrandom pattern of species distributions. In particular, some species pairs may never be found in the same community due to competitive exclusion. Rigorous analytical methods have been developed to investigate the possible role that interspecific competition has on the evolution of communities. Many studies that have implemented these methods have shown support for Diamond's assembly rules, yet there are numerous exceptions. We build on this previous research by examining the co-occurrence patterns of primate species in 109 communities from across the world. We used EcoSim to calculate a checkerboard (*C*) score for each region. The *C* score provides a measure of the propor-

tion of species pairs that do not co-occur in a set of communities. High *C* scores indicate that species are nonrandomly distributed throughout a region, and interspecific competition may be driving patterns of competitive exclusion. We conducted two sets of analyses. One included all primate species per region, and the second analysis assigned each species to one of four dietary guilds: frugivores, folivores, insectivores, and frugivore-insectivores. Using all species per region, we found significantly high *C* scores in 9 of 10 regions examined. For frugivores, we found significantly high-*C* scores in more than 50% of regions. In contrast, only 23% of regions exhibited significantly high-*C* scores for folivores. Our results suggest that communities are nonrandomly structured and may be the result of greater levels of interspecific competition between frugivores compared to folivores. *Am J Phys Anthropol* 144:131–139, 2011. © 2010 Wiley-Liss, Inc.

A fundamental research focus in community ecology involves the factors that influence community structure. Environmental variables are commonly examined to predict various aspects of animal communities, such as species richness and species composition (Currie, 1991; Andrews and O'Brien, 2000; Reed and Bidner, 2004; Kamilar, 2009). For primates, as well as other vertebrates, previous research has shown that there is a positive correlation between mean annual rainfall and species richness (Reed and Fleagle, 1995; Kay et al., 1997; Hawkins et al., 2003). Annual rainfall is often related to plant productivity, which forms the dietary resource base for numerous vertebrates. Additional factors, such as tree height, canopy volume, predation, and human-induced habitat disturbance, can influence the diversity of members of a community (Reed and Bidner, 2004). Furthermore, phylogenetic history and biogeographic factors have been suggested to strongly influence species distributions, mostly through historical patterns of species dispersal and/or vicariance (Cracraft, 1994; Fleagle and Reed, 1999; Lawes and Eeley, 2000; Hawkins and Porter, 2003; Kamilar, 2009; Kamilar and Guidi, 2010).

Although difficult to test without an experimental approach, interspecific competition has also been invoked as an important factor shaping broad-scale variation in community structure. Diamond (1975) and others [e.g., Fox and Brown (1993)] have proposed community assembly rules that are based on the idea that interspecific competition governs the presence and absence of species in communities. Some studies have used primates as a model

taxon to test this hypothesis. For example, Ganzhorn (1997) found that Malagasy primate communities followed Fox's assembly rule (Fox, 1987). This suggests that competition between members of a community results in favoring entry to only those species that are most ecologically distinct from current members of the community, such that each functional group is represented by an equivalent number of species before additional members are allowed entry (Fox, 1987; Fox and Brown, 1993). Although interspecific competition has been commonly invoked as the mechanism producing this pattern, Wilson (1995) showed that a similar scenario may be produced by randomly assigning species to communities.

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

Grant sponsor: NSF Dissertation Improvement awarded to JMK; Grant number: BCS-0452814.

*Correspondence to: Jason M. Kamilar, Department of Anthropology, Yale University, New Haven, Connecticut 06520-8277. E-mail: jason.kamilar@yale.edu

Received 23 February 2010; accepted 18 June 2010

DOI 10.1002/ajpa.21380

Published online 25 August 2010 in Wiley Online Library (wileyonlinelibrary.com).

TABLE 1. Sample sizes used in this study

Region ^a	No. communities	No. total species	No. frugivore species	No. folivore species	No. insectivore species	No. frugivore-insectivore species
East Africa	20	28	14	4	10	<i>x</i>
Central Africa	11	33	20	5	7	<i>x</i>
West Africa	8	25	16	<i>x</i>	6	<i>x</i>
Central Amazon	5	29	20	<i>x</i>	<i>x</i>	5
West Amazon	10	30	24	<i>x</i>	<i>x</i>	5
Guyana Shield	7	13	10	<i>x</i>	<i>x</i>	<i>x</i>
East Madagascar	17	23	6	9	<i>x</i>	4
West Madagascar	13	24	5	5	<i>x</i>	9
Mainland Southeast Asia	11	17	7	8	<i>x</i>	<i>x</i>
Sunda Shelf	7	15	6	7	<i>x</i>	<i>x</i>

x indicates that sample size was too small to analyze.

^aThe same species may be found in different regions within each continent.

An assembly rule proposed by Diamond (1975), one that has been surrounded by a great deal of controversy, involves the nonrandom occurrence of species in “checkerboard” distributions. He argued that in a set of communities, interspecific competition in the past results in the absence of one species being associated with the presence of another in a nonrandom fashion. Connor and Simberloff (1979) suggested that the assembly rules proposed by Diamond (1975) were tautologies and that checkerboard distributions could very well arise in communities with little or no interspecific competition. Some of the early problems with testing Diamond’s predictions were methodological. Rigorous statistical analyses to properly test whether species co-occurrence patterns are nonrandom have been improved during the past 15–20 years (Atmar and Patterson, 1993; Colwell, 1999; Gotelli and Entsminger, 2009). During this time, a number of studies have added support to Diamond’s (1975) hypotheses (Stone and Roberts, 1990; Manly, 1995; Gotelli et al., 1997; Sanderson et al., 1998; Gotelli, 2000; Gotelli and McCabe, 2002), yet the mechanisms producing these patterns of species distributions are still not always easy to discern.

Primates provide an ideal group to examine questions related to competition and community structure. Intraspecific dietary competition has long been considered a driving force shaping primate social structure (van Schaik and van Hooft, 1983; Janson, 1988) and group size (Janson, 1992; Wrangham et al., 1993). Furthermore, food competition is expected to be high when dietary resources are relatively rare and/or defensible and low when they are abundant and/or indefensible (Janson, 1988). Traditionally, frugivorous species are thought to experience greater food competition compared to folivores, because fruits are regarded as rare and/or defensible resources (Sterck et al., 1997). However, recent research has challenged this idea, suggesting that some folivorous primates compete for access to preferred leaves (Koenig, 2000; Snaith and Chapman, 2007). There are several studies that suggest spatial patterns on small and large scales are mediated by interspecific competition between primate species that occupy similar niches (Porter, 2001; Buzzard, 2006; Lehman, 2006).

In this study, we used a broad-scale approach to investigate whether the distribution patterns of primates in African, Malagasy, South American, and Asian communities are consistent with Diamond’s (1975) assembly rules, exhibiting nonrandom patterns of species co-occurrence. We also investigated co-occurrence patterns within and between dietary guilds to better test if com-

petition was the mechanism driving nonrandom species distributions. Based on previous research examining competition for different dietary resources, we predicted that checkerboard patterns of species distributions will be more common for taxa that eat rare and/or defensible foods (e.g., fruit and insects) compared to those preferring more widely available resources (e.g., leaves), due to higher levels of interspecific competition among frugivores (Lehman, 2006). Strong competitive interactions in the past should produce numerous cases of competitive exclusion in modern communities, leading to checkerboard patterns of species distributions.

METHODS

We used published presence–absence species lists (Kamilar, 2009) collated from 109 study sites across Africa (39), South America (22), Madagascar (30), and Asia (18) (Table 1, Fig. 1, and Supporting Information 1). We did not examine species co-occurrence patterns at the continental level, because historical factors such as dispersal and vicariance are likely to influence species distributions and confound any effects due to interspecific competition (Kamilar, 2009; Kamilar et al., 2009). Instead, we analyzed the data at the regional level, with each continent divided into separate biogeographic areas of endemism based on Kamilar (2009) (Table 1 and Fig. 1). Kamilar’s (2009) areas of endemism were based on an Unweighted Pair Group Method with Arithmetic Mean cluster analysis of the presence–absence of species in each continent. Several regions within each continent were relatively distinct from others based on their species compositions [see Figs. 3–6 in Kamilar (2009)]. Using this scheme, our dataset contained three regions in Africa (East, Central, and West), three regions in South America (Central Amazon, West Amazon, and Guyana Shield), two regions in Madagascar (East and West), and two regions in Asia (Mainland Southeast Asia and the Sunda Shelf) (Table 1). Data from other regions within each continent were available but were not included, because the number of species and/or sites in these regions was too small for statistical analysis.

We used the EcoSim software package (Gotelli and Entsminger, 2009) to test for nonrandom patterns of species co-occurrence. EcoSim allows users to test for patterns in species communities by comparing real presence–absence data matrices to randomly generated “pseudo-communities” (Pianka, 1986). Although there

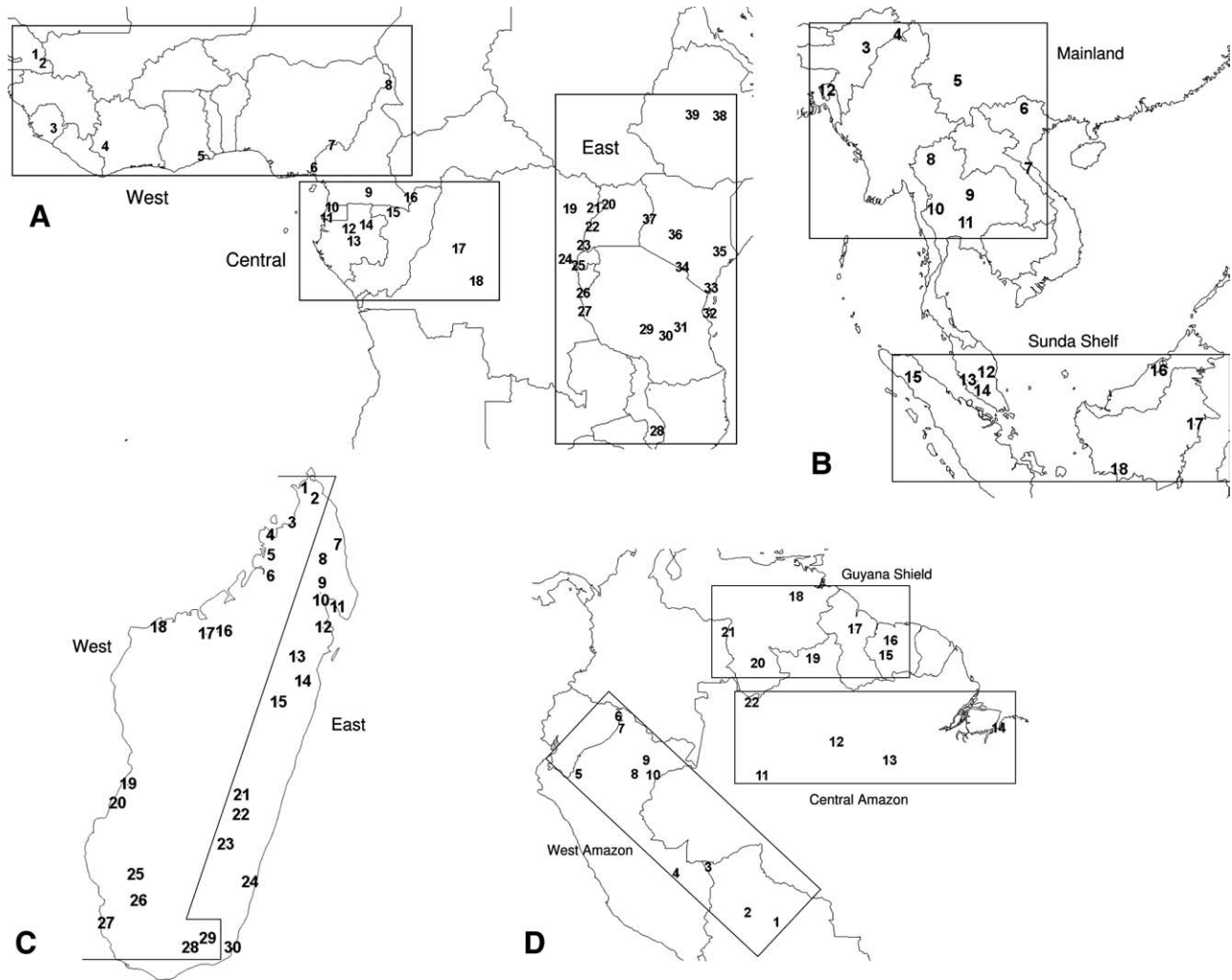


Fig. 1. The location of primate communities and areas of endemism included in our study. **A:** African communities: (1) Assirik, (2) Kedougou, (3) Tiwai, (4) Tai, (5) Shai Hills, (6) Korup, (7) Kilum-Ijim, (8) Waza, (9) Dja, (10) Monte Alen, (11) Rio Muni, (12) Lope, (13) Makande, (14) Makakou, (15) Odzala, (16) Mondika, (17) Nyungwe, (18) Salonga, (19) Lukuru, (20) Ituri, (21) Budongo, (22) Semliki-Toro, (23) Kibale, (24) Bwindi, (25) Kahuzi-Biega, (26) Gombe, (27) Mahale, (28) Zomba, (29) Ruaha, (30) Uzungwa, (31) Mikumi, (32) Jozani, (33) Diani Beach, (34) Amboseli, (35) Tana, (36) Laikipia, (37) Kakamega, (38) Awash, (39) Bole. **B:** Asian communities: (1) Sepahijala, (2) Gumti, (3) Hollongapar, (4) Namdapha, (5) Wuliang, (6) Na Hang, (7) Huong Khe, (8) Doi Suthep-Pui, (9) Phu Khieo, (10) Huai Kha Khaeng, (11) Khao Yai, (12) Sungai Tekam, (13) Ulu Sempam, (14) Kuala Lumpur, (15) Ketambe, (16) Gunung Mulu, (17) Kutai, (18) Tanjung Putting. **C:** Malagasy communities: (1) Montage d'Ambre, (2) Analamera, (3) Manehoko, (4) Manongarivo, (5) Mahilaka, (6) Bora, (7) Marojejy, (8) Anjanaharibe, (9) Amparihibe, (10) Ankirindro, (11) Andranobe, (12) Verezantsoro, (13) Zahamena, (14) Betampona, (15) Analamazaotra, (16) Ankarafantsika, (17) Madirovalo, (18) Namoroka, (19) Andranomena, (20) Kirindy, (21) Vohibola III, (22) Ranomafana, (23) Andringitra, (24) Manombo, (25) Zombitse, (26) Beza-Mahafaly, (27) Tsimanampetsotsa, (28) Berenty, (29) Andohahela, and (30) Ste. Luce. **D:** Neotropical communities: (1) El Triunfo, (2) Beni, (3) San Sebastian, (4) Manu, (5) Rio Cenepa, (6) Yasuni, (7) Tambocha, (8) Saimiria, (9) Camp Callicebus, (10) Quebrada Blanco, (11) Rio Urucu, (12) Manaus, (13) Tapajos, (14) Belem, (15) Nourages, (16) Raleighvallen-Voltzburg, (17) Mabura, (18) Guri Lake, (19) Maracá, (20) Esmeralda, (21) Puerto Ayacucho, and (22) Pico da Neblina.

are several metrics available to quantify co-occurrence patterns, we chose Stone and Robert's (1990) checkerboard score (C score). The C score quantifies the mean number of "checkerboard units" among all possible pairs of species in a presence-absence matrix (Gotelli and Entsminger, 2009). Sanders et al. (2003) state that a "checkerboard unit" is represented by a 2×2 submatrix (e.g., two species by two sites), where a species pair does not co-occur (see Fig. 2). If the presence-absence data matrices have a significantly higher C score than randomly generated matrices, then a substantial number of species pairs co-occur less often than by chance, suggesting that spatial distributions may be structured by inter-

specific competition. Alternatively, significantly, low- C scores suggest that several species co-occur more frequently than expected by chance. Finally, if interspecific competition is not important, then observed C scores should not differ from randomly generated ones (see Fig. 2 for an illustration of these different scenarios).

We calculated statistical significance by generating 5000 random data matrices and tested whether the C score of the real presence-absence data matrix was greater than 95% of the highest or less than 95% of the lowest C scores from the randomly generated datasets. Our data are most similar to Gotelli's (2000) "island lists," which contain complete lists of all species on an

Example A	Site A	Site B	Site C	Site D	Site E
Species1	X		X	X	
Species2	X	X	X		X
Species3		X		X	
Species4	X	X		X	
Species5	X		X		
Species6		X	X	X	X

Example B	Site A	Site B	Site C	Site D	Site E
Species1	X		X	X	
Species2		X			X
Species3	X	X			X
Species4				X	
Species5	X		X	X	
Species6		X			X

Example C	Site A	Site B	Site C	Site D	Site E
Species1	X		X	X	
Species2	X	X	X	X	
Species3	X	X	X		
Species4				X	X
Species5	X	X		X	X
Species6	X	X		X	X

*An X denotes the presence of a species at a site

Fig. 2. Example A illustrates a checkerboard (*C*) score no different than random because species do not co-occur more or less than expected by chance (i.e., species are randomly distributed across sites). Example B illustrates a significantly high *C* score, because several species pairs co-occur less than expected by chance (i.e., they are rarely or never found in the same community). The shaded area of the matrix represents a checkerboard unit. Example C demonstrates a significantly low *C* score because several species co-occur more often than random.

island or from a distinct habitat patch. Therefore, we followed Gotelli's (2000) suggestion to maintain the same number of species for each site and the same number of sites for each species when generating random datasets to calculate statistical significance (Connor and Simberloff, 1979). In addition, Gotelli (2000) suggested that using *C* scores reduces the amount of Type I and Type II error and is particularly suited for "island list" data. Unfortunately, the EcoSim software does not tell us which species pairs or communities are most important for driving species co-occurrence patterns within a set of communities, though some of these patterns may be gleaned from examining the data matrix (see Supporting Information 1). It is important to note that we used one model in our analysis and other models exist. Further testing is needed to determine the possible effects of different models for the results of null model analysis [e.g., see Maestre et al. (2008)].

Because interspecific competition for dietary resources may play a particularly important role in driving species distributions, we conducted a second set of analyses examining species co-occurrence patterns in different dietary guilds. A guild can be defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root, 1967). We defined our

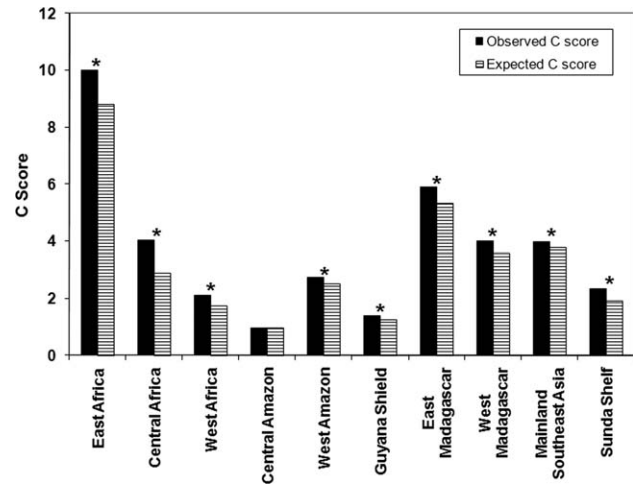


Fig. 3. Bar chart illustrating the observed and expected *C* (checkerboard) scores for all regions using all species per region. Statistically significant ($P < 0.05$) checkerboard scores are marked by an asterisk and indicate that numerous species pairs do not co-occur. A randomization approach was implemented to calculate statistical significance. Therefore, the magnitude of the difference between observed and expected *C* scores is more important than absolute *C* score values.

dietary guilds in a similar fashion to those presented in Nunn (2002a,b), because most of our dietary data were obtained from those papers. We assigned species to one of four dietary guilds: (1) frugivore, (2) folivore, (3) insectivore, and (4) frugivore–insectivore. We considered additional dietary guilds to include in the analyses (e.g., folivore–frugivore), but too few species occupied these groups to conduct statistical tests.

Dietary data for Malagasy lemurs and species missing from Nunn (2002a,b) were obtained from Walker (1975), Charles-Dominique (1977), Ganzhorn et al. (1985), Meier et al. (1987), Harcourt and Thornback (1990), Ganzhorn (1993, 1997), Mittermeier et al. (1994), Sterling et al. (1994), Garbutt (1999), Nowak (1999), Vasey (2003), and Lehman and Fleagle (2006). If a species supplemented its diet with 30% or more from a different type of food, it was assigned the dual-diet guild (e.g., if a species fed mainly on fruits but also included 30% or more insects in its diet it would be classified as a "frugivore–insectivore").

We examined the degree of species co-occurrence in each dietary guild individually by running each species-diet matrix in the co-occurrence analysis, and calculating observed versus expected *C* scores. These totaled 23 separate analyses, because each dietary guild was not represented in each biogeographic region.

RESULTS

Co-occurrence patterns of primates

When we examined all species in each region, we found significantly high *C* scores in nine of the 10 biogeographic zones (see Fig. 3). This indicates that within each biogeographic region, species are often found in checkerboard distributions (i.e., many members of species-pairs will not occur together). The strongest checkerboard distributions were found in Africa, with all three regions exhibiting significant high *C* scores at the $P < 0.001$ level. Two of the three areas in the Neotropics displayed significant checkerboard patterns (Guyana

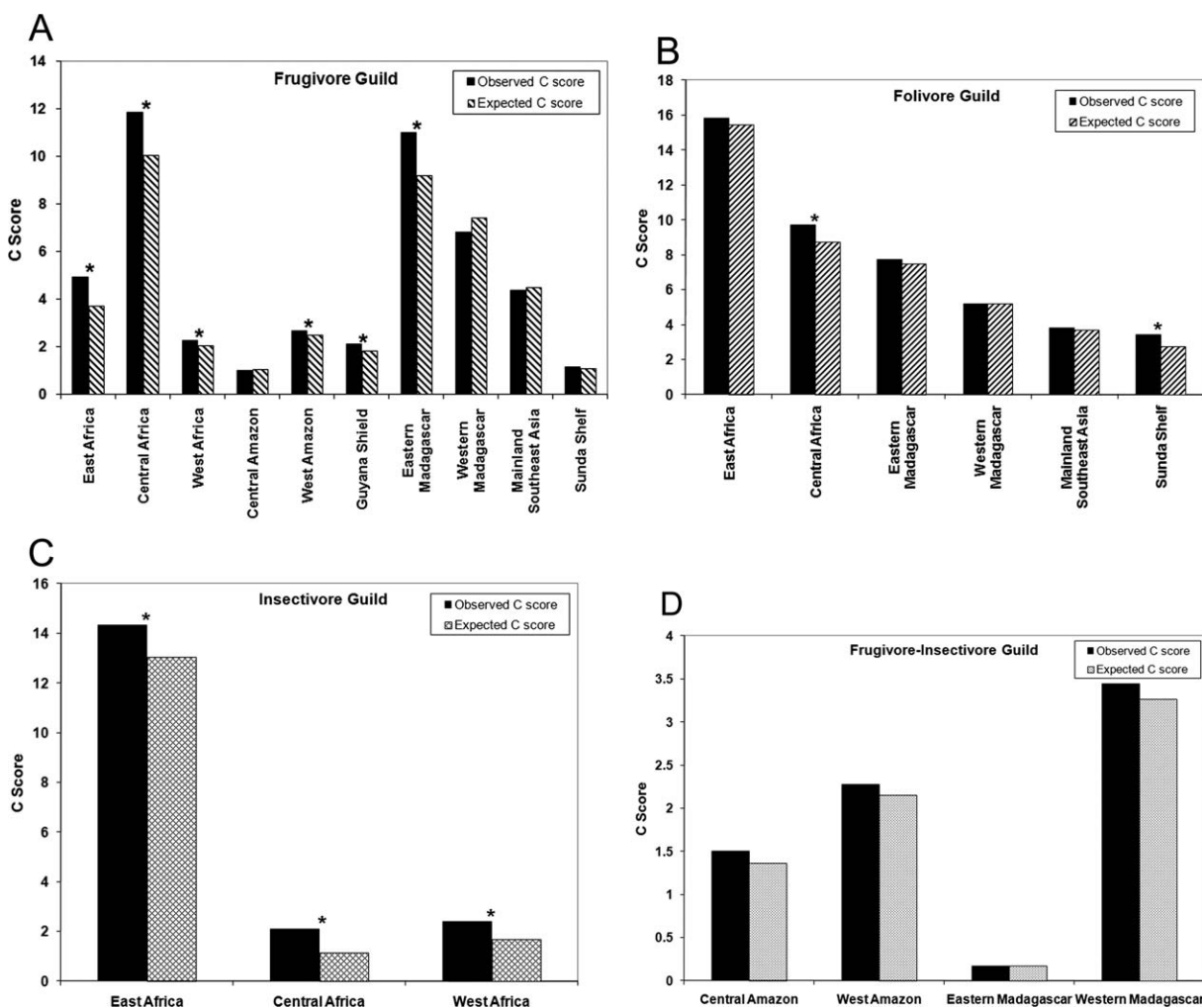


Fig. 4. Bar chart illustrating the observed and expected *C* (checkerboard) scores for species in the following dietary guilds: (A) frugivores, (B) folivores, (C) insectivores, and (D) frugivore-insectivores. Statistically significant ($P < 0.05$) checkerboard scores are marked by an asterisk and indicate that numerous species pairs do not co-occur. A randomization approach was implemented to calculate statistical significance. Therefore, the magnitude of the difference between observed and expected *C* scores is more important than absolute *C* score values.

Shield, $P = 0.015$ and West Amazon, $P < 0.001$), yet species were randomly distributed in the Central Amazon region. Significantly, high *C* scores were also found in both regions within Madagascar ($P < 0.001$ for the East and West region) and Asia (Mainland, $P = 0.019$ and Sunda Shelf, $P < 0.001$).

Co-occurrence patterns within and between primate dietary guilds

We found mixed results when we examined the co-occurrence patterns of species in different dietary guilds. For many of these analyses, species exhibited co-occurrence patterns that were not significantly different than random. However, *C* scores for frugivores were significantly high in six of the 11 regions (55%) (Fig. 4A). In contrast, only two of the 10 regions (20%) produced significantly high *C* scores for folivores, with the remaining regions no different from random (Fig. 4B). The Sunda Shelf folivores exhibited significantly high *C* scores, whereas frugivorous and insectivorous species in that region did not. We also found that all three regions con-

taining insectivore guilds exhibited significantly high *C* scores (Fig. 4C). Finally, *C* scores were random for the frugivore–folivore dietary guilds in all four regions where data were available (Fig. 4D).

DISCUSSION

Without accounting for species' dietary niche characteristics, we found that there were a significant amount of checkerboard species distributions in all regions except for the Central Amazon. These results add support to Diamond's hypothesis (1975) that communities are nonrandomly structured and suggest that the presence or absence of species is affected by interspecific competition. High levels of interspecific competition in the past would result in certain species pairs rarely or never occurring in the same present-day community. Our findings are also concordant with a meta-analysis of 96 presence–absence datasets from a wide range of taxa (Gotelli and McCabe, 2002). The authors found statistically significant checkerboard patterns for all datasets, yet the standardized effect of these co-occurrence pat-

terns varied across taxa. Although the Gotelli and McCabe (2002) study, as well as ours, found significant nonrandom patterns of species distribution, ascribing the mechanism producing these patterns is not definitive.

Our analysis examining co-occurrence patterns within dietary guilds more directly examines the possibility that interspecific competition is the mechanism driving species distributions. We found differences in the co-occurrence patterns between dietary guilds. Species belonging to the frugivorous and insectivorous dietary guilds exhibited significant *C* scores in the majority of regions examined. This finding suggests that species filling these dietary niches experience high levels of interspecific competition (Struhsaker, 1978). Although studies of primate communities have often focused on niche separation between sympatric species to explain coping with competition over limited resources (Gautier-Hion, 1980; Terborgh, 1983; Garber and Sussman, 1984; Ganzhorn, 1989), others have hypothesized that strong interspecific competition can also effect the presence or absence of species in primate communities. For example, Lehman (2000) suggested that closely related *Cebus* species were rarely found sympatrically in Guyanan communities because of competitive exclusion due to past interspecific competition driven by a high degree of niche overlap.

In contrast, species designated as folivores or frugivore-insectivores did not co-occur more or less than expected in most regions analyzed. This suggests that folivorous primates compete less for dietary resources with species occupying a similar dietary niche. In addition, our results suggest that primates that broaden their diet by feeding on a significant amount of both fruits and insects may experience less interspecific competition for limited resources.

Although the majority of frugivore guilds fit our prediction that these species would co-occur less frequently than random, there were some regions that did not meet this expectation. In Madagascar and Asia, only one of the four total regions displayed significantly high *C* scores for frugivores. This may be partly due to the particular frugivore species that are endemic to these regions. For instance, many of the Asian primates that we designated as frugivores are often considered ecological generalists (e.g., *Macaca*), consuming a wide range of dietary items (Fooden, 1980; Richard et al., 1989; Ross et al., 1993). This may allow greater niche separation for these species compared to more specialized frugivores found in Africa and the Neotropics.

We examined both frugivore and folivore guilds in six regions. We found that species of both guilds were randomly distributed in two of these regions, western Madagascar and mainland Southeast Asia. This suggests that food competition may have been a lesser factor structuring communities in these regions. Unlike the Neotropics, many Malagasy primates are folivorous (Fleagle and Reed, 1996). This may be the result of an extended dry season, the high frequency of droughts, which affect resource availability (Reed and Bidner, 2004), or the lack of protein in the fruit consumed by primates (Ganzhorn et al., 2009). In addition, the relatively few fruit-eating taxa in the western rainforest of Madagascar may contribute to the random co-occurrence patterns in this region. In our dataset, many mainland Southeast Asian communities have relatively low levels of primate species richness, which may result in lower levels of interspecific competition (Struhsaker, 1978), because there are fewer

species that may be potential competitors. However, species' population density values may be a more critical factor. In addition, these communities contain several macaque species, which are often regarded as ecological generalists. Macaques occupy a variety of habitat types, use numerous vertical zones within each habitat, and consume a wide variety of food types (Crockett and Wilson, 1980; Fooden, 1982; Fa and Lindburg, 1996). These strategies likely reduce interspecific competition.

Our finding that a significantly high *C* score was present for folivores on the Sunda Shelf was unexpected and may be related to increased interspecific dietary competition due to a combination of high levels of folivore species richness and strong selectivity for leaves. Folivore species richness in Asia is only exceeded by Eastern Malagasy communities. Some recent evidence suggests that folivores may actually be quite selective about the quality of leaves that they eat, often feeding on high-quality immature leaves, which are distributed in small patches (Snaith and Chapman, 2007). In addition, previous research has shown a correlation between folivore biomass and leaf quality, suggesting that leaves are sometimes a limiting factor (Oates et al., 1990; Ganzhorn, 1992; Chapman et al., 2002). These findings suggest higher levels of food competition among folivores than traditionally thought. Also, many Asian forests are dominated by Dipterocarp trees, which are not a preferred food source of leaf monkeys (Davies, 1991; Kool, 1993). The combination of these factors may have led to increased competition among folivores in the Sunda Shelf.

Defining dietary guilds

It is essential to note that our definition of dietary guilds is broad but was needed to maximize the number of species included in our study. Our broad dietary categories do not capture potentially important variation that may be essential for understanding interspecific competition. Foods that seemingly belong to the same dietary category may have drastically different chemical and physical properties, which may require different morphological adaptations (van Roosmalen, 1984). For example, Kinzey and Norconk (1993) suggested that niche separation was a central aspect of pitheciine ecology. They found that sympatric *Pithecia pithecia* and *Chiropotes satanas* are able to co-exist with limited competition over fruit by exploiting fruits at different stages of ripeness.

In addition, broad dietary categories may not capture the level of dietary variation within a particular species. For example, some colobine monkeys, which are considered leaf specialists, have exhibited drastic seasonal shifts in diet, with almost 80% of their diet comprising fruit and seeds in some months (Koenig and Borries, 2001). In addition, although all colobine monkeys have anatomical specializations adapted for processing leaves, there is substantial interspecific variation in the types of leaves consumed. Kamilar and Paciulli (2008) illustrated this point by showing a negative relationship between the percentage of mature leaves in the diet of colobine monkeys and their risk of extinction. This suggests that species consuming less preferred foods such as mature leaves are better able to maintain their population size. No effect was found with the amount of young leaf intake.

Furthermore, competition between orders, or even classes, is often not considered (Simberloff and Dayan, 1991). It is possible that considerable competition exists between primates and other animals. For example, sym-

patric *Chiropotes satanas* and *Ara chloroptera* (red and green macaw) in Venezuela may compete for the seeds of unripe fruits (Norconk et al., 1997). Unfortunately, without a complete list of every food eaten by every living primate and nonprimate species and quantitative chemical and material property data for those foods, we are limited to such broad dietary categories.

Additional factors influencing species co-occurrence patterns

Sample size may also influence the *C* scores generated for the different regions and/or dietary guilds. As in any test, statistical power decreases with decreasing sample size. Consequently, it is possible that sample-size differences between the frugivore and folivore guilds have impacted the differences in *C* scores between these groups. The higher *C* scores for frugivores compared to folivores may be due to the fact that most regions contain more frugivorous species. Yet, we did find numerous cases where small samples sizes produced significantly high *C* scores. All three regions where insectivore guilds were examined produced significantly high *C* scores, and the sample sizes in these regions were comparable to folivores. In addition, the folivores in Central Africa exhibited a significant *C* score, yet had the second smallest sample size. Because of these examples, we do not feel that sample size was the driving factor causing the differences in *C* scores between frugivores and folivores.

Besides interspecific competition, there are other factors that may affect co-occurrence patterns and *C* scores. For instance, the significantly high *C* scores among folivores in the Sunda Shelf may also have been generated by biogeographic history. The diverse numbers of folivorous monkeys in this region are found in forested areas, which have expanded and contracted numerous times during the past several million years (Harrison et al., 2006). In addition, the size and connectivity of islands comprising the Sunda Shelf have undergone substantial changes corresponding to sea levels rising and falling (Harrison et al., 2006). Both these scenarios have likely played a significant role in the allopatric speciation of numerous folivore species, being endemic to particular islands/regions within the Sunda Shelf (Harrison et al., 2006; Kamilar, 2009). Consequently, it is possible that biogeographic factors have influenced the distribution of species in this region as well as others (Lawes and Eeley, 2000; Kamilar, 2009), resulting in several species pairs never occurring in the same community.

In addition to biogeographic history, our findings do not minimize the importance of anthropogenic effects (Harcourt and Parks, 2003), predation (Isbell, 1990), and climatic and habitat characteristics (Reed and Fleagle, 1995; Kay et al., 1997; Peres and Janson, 1999) for influencing species distributions. Finally, modern primate communities contain species that are ecologically similar along several niche axes yet still coexist by adapting several strategies, such as using different forest strata, seasonally shifting their food preferences, or spending more time in different microhabitats within a field site (Schreier et al., 2009).

ACKNOWLEDGMENTS

We thank Andreas Koenig, Kerry Ossi, Lisa Guidi, Kathleen Muldoon, and two anonymous reviewers for helpful comments that improved earlier versions of this work.

LITERATURE CITED

- Andrews P, O'Brien EM. 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J Zool* 251:205–231.
- Atmar W, Patterson BD. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–382.
- Buzzard PJ. 2006. Ecological partitioning of *Cercopithecus campbelli*, *Cercopithecus petaurista*, and *Cercopithecus diana* in the Tai Forest. *Int J Primatol* 27:529–558.
- Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002. Application of protein-to-fiber ratios to predict colobine abundance on difference spatial scales. *Int J Primatol* 23:283–310.
- Charles-Dominique P. 1977. Ecology and behavior of nocturnal prosimians. New York: Columbia University Press.
- Colwell RK. 1999. EstimateS. Statistical estimation of species richness and shared species from samples. Version 5.0.1.:http://viceroy.eeb.uconn.edu/EstimateS.
- Connor EF, Simberloff D. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132–1140.
- Cracraft J. 1994. Species diversity, biogeography, and the evolution of biotas. *Am Zool* 34:33–47.
- Crockett CM, Wilson WL. 1980. The ecological separation of *Macaca nemestrina* and *M. fascicularis* in Sumatra. In: Lindburg DG, editor. The macaques: studies in ecology, behavior and evolution. New York: Van Nostrand Reinhold. p 148–181.
- Currie D. 1991. Energy and large-scale patterns of animal- and plant- species richness. *Am Nat* 137:27–49.
- Davies G. 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern Borneo. *Int J Primatol* 12:119–144.
- Diamond JM. 1975. Assembly of species communities. In: Cody ML, Diamond JM, editors. Ecology and evolution of communities. Cambridge: Belknap. p 342–444.
- Fa JE, Lindburg DG. 1996. Evolution and ecology of macaque societies. Cambridge: Cambridge University Press.
- Fleagle JG, Reed KE. 1996. Comparing primate communities: a multivariate approach. *J Hum Evol* 30:489–510.
- Fleagle JG, Reed KE. 1999. Phylogenetic and temporal perspectives on primate ecology. In: Fleagle JG, Janson C, Reed KE, editors. Primate communities. New York: Cambridge University Press. p 92–115.
- Fooden J. 1980. Classification and distribution of living macaques (*Macaca leapede*, 1799). In: Lindburg DG, editor. The macaques: studies in ecology, behavior and evolution. New York: Van Nostrand Reinhold. p 1–9.
- Fooden J. 1982. Ecogeographic segregation of macaque species. *Primates* 23:574–579.
- Fox BJ. 1987. Species assembly and the evolution of community structure. *Evol Ecol* 1:201–213.
- Fox BJ, Brown JH. 1993. Assembly rules for functional groups in North American desert rodent communities. *Oikos* 67:358–370.
- Ganzhorn JU. 1989. Niche separation of seven lemur species in eastern rainforest of Madagascar. *Oecologia* 79:279–286.
- Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests: test of a hypothesis. *Oecologia* 91:540–547.
- Ganzhorn JU. 1993. Flexibility and constraints of *Lepilemur* ecology. In: Kappeler P, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 153–166.
- Ganzhorn JU. 1997. Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. *J Zool (Lond)* 241:533–542.
- Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M. 1985. Some aspects of the natural history and food selection of *Avahi laniger*. *Primates* 26:452–463.
- Ganzhorn JU, Arrigo-Nelson S, Boinski S, Bollen A, Carrai V, Derby A, Donati G, Koenig A, Kowalewski M, Lahann P, Norscia I, Polowinsky SY, Schwitzer C, Stevenson PR, Talebi MG, Tan C, Vogel ER, Wright PC. 2009. Possible fruit protein effects on primate communities in Madagascar and the Neo-

- tropics. PLoS ONE 4:e8253; doi:8210.1371/journal.pone.0008253.
- Garber PA, Sussman RW. 1984. Ecological distinctions between sympatric species of *Saguinus* and *Sciurus*. *Am J Phys Anthropol* 65:135–146.
- Garbutt N. 1999. *Mammals of Madagascar*. New Haven: Yale University Press.
- Gautier-Hion G. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J Anim Ecol* 49:237–269.
- Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- Gotelli NJ, Buckley NJ, Wiens JA. 1997. Co-occurrence of Australian land birds: diamond's assembly rules revisited. *Oikos* 80:311–324.
- Gotelli NJ, Entsminger GL. 2009. EcoSim: null models software for ecology. Version 7.0. Acquired Intelligence Inc & Kesey-Bear: <http://garyentsminger.com/ecosim.htm>.
- Gotelli NJ, McCabe DJ. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecol Lett* 83:2091–2096.
- Harcourt AH, Parks SA. 2003. Threatened primates experience high human densities: adding an index of threat to the IUCN Red List criteria. *Biol Conserv* 109:137–149.
- Harcourt C, Thornback J. 1990. *Lemurs of Madagascar and the Comoros: The IUCN Red Data Book*. Gland, Suisse: IUCN.
- Harrison T, Krigbaum J, Manser J. 2006. Primate biogeography and ecology on the Sunda Shelf islands: a paleontological and zooarchaeological perspective. In: Lehman S, Fleagle JG, editors. *Primate biogeography*. New York: Springer. p 331–374.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Hawkins BA, Porter EE. 2003. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecol Biogeogr* 12:475–481.
- Isbell LA. 1990. Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Am J Primatol* 21:41–52.
- Janson CH. 1988. Intra-specific food competition and primate social structure: a synthesis. *Behaviour* 105:71–79.
- Janson CH. 1992. Evolutionary ecology of primate social structure. In: Smith EA, Winterhalder B, editors. *Evolutionary ecology and human behavior*. New York: Aldine de Gruyter. p 95–130.
- Kamilar JM. 2009. Environmental and geographic correlates of the taxonomic structure of primate communities. *Am J Phys Anthropol* 139:382–393.
- Kamilar JM, Guidi LM. 2010. The phylogenetic structure of primate communities: variation within and across continents. *J Biogeogr* 37:801–813.
- Kamilar JM, Martin SK, Tosi AJ. 2009. Combining biogeographic and phylogenetic data to examine primate speciation: an example using guenon monkeys. *Biotropica* 41:514–519.
- Kamilar JM, Paciulli LM. 2008. Examining the extinction risk of specialized folivores: a comparative study of colobine monkeys. *Am J Primatol* 70:1–12.
- Kay RF, Madden RH, van Schaik C, Higdon D. 1997. Primate species richness is determined by plant productivity: implications for conservation. *Proc Natl Acad Sci USA* 94:13023–13027.
- Kinzey WG, Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int J Primatol* 14:207–227.
- Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behav Ecol Sociobiol* 48:93–109.
- Koenig A, Borries C. 2001. Socioecology of Hanuman langurs: the story of their success. *Evol Anthropol* 10:122–137.
- Kool KM. 1993. The diet and feeding-behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *Int J Primatol* 14:667–700.
- Lawes MJ, Eeley HAC. 2000. Are local patterns of anthropoid primate diversity related to patterns of diversity at a larger scale? *J Biogeogr* 27:1421–1435.
- Lehman SM. 2000. Primate community structure in Guyana: a biogeographic analysis. *Int J Primatol* 21:333–351.
- Lehman SM. 2006. Nested distribution patterns and the historical biogeography of the primates of Guyana. In: Lehman SM, Fleagle JG, editors. *Primate biogeography*. New York: Springer. p 63–80.
- Lehman SM, Fleagle JG. 2006. *Primate biogeography*. New York: Springer.
- Maestre FT, Escobar C, Martínez I, Escudero A. 2008. Are soil lichen communities structured by biotic interactions? A null model analysis. *J Veg Sci* 19:261–263.
- Manly BFJ. 1995. A note on the analysis of species co-occurrence. *Ecology* 76:1109–1115.
- Meier B, Albignac R, Peyriéras A, Rumpler Y, Wright P. 1987. A new species of *Haplemur (Primates)* from south east Madagascar. *Folia Primatol* 48:211–215.
- Mittermeier RA, Tattersall I, Konstant WR, Meyers DM, Mast RB. 1994. *Lemurs of Madagascar*. Washington, D. C.: Conservation International.
- Norconk MA, Wertis C, Kinzey WG. 1997. Seed predation by monkeys and macaws in eastern Venezuela: preliminary findings. *Primates* 38:177–184.
- Nowak R. 1999. *Walker's mammals of the world*. Baltimore: The Johns Hopkins University Press.
- Nunn CL. 2002a. A comparative study of leukocyte counts and disease risk in primates. *Evolution* 56:177–190.
- Nunn CL. 2002b. Spleen size, disease risk and sexual selection: a comparative study in primates. *Evol Ecol Res* 4:91–107.
- Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from west Africa. *Ecology* 71:328–343.
- Peres C, Janson C. 1999. Species coexistence, distribution, and environmental determinants of Neotropical primate richness: a community-level zoogeographic analysis. In: Fleagle J, Janson C, Reed K, editors. *Primate communities*. Cambridge: Cambridge University Press. p 55–74.
- Pianka ER. 1986. *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton: Princeton University Press.
- Porter LM. 2001. Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *Int J Primatol* 22:961–992.
- Reed K, Fleagle JG. 1995. Geographic and climatic control of primate diversity. *Proc Natl Acad Sci USA* 92:7874–7876.
- Reed KE, Bidner LR. 2004. Primate communities: past, present, and possible future. *Am J Phys Anthropol* 47:2–39.
- Richard AF, Goldstein SJ, Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. *Int J Primatol* 10:569–594.
- Root R. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol Monogr* 37:317–350.
- Ross C, Srivastava A, Pirta RS. 1993. Human influences on the population density of Hanuman langurs *Presbytis entellus* and Rhesus macaques *Macaca mulatta* in Shimla, India. *Biol Conserv* 65:159–163.
- Sanders NJ, Gotelli NJ, Heller NE, Gordon DM. 2003. Community disassembly by an invasive species. *Proc Natl Acad Sci USA* 100:2474–2477.
- Sanderson JG, Moulton MP, Selfridge RG. 1998. Null matrices and the analysis of species co-occurrences. *Oecologia* 116:275–283.
- Schreier BM, Harcourt AH, Coppeto SA, Somi MF. 2009. Interspecific competition and niche separation in primates: a global analysis. *Biotropica* 41:283–291.
- Simberloff D, Dayan T. 1991. The guild concept and the structure of ecological communities. *Ann Rev Ecol Syst* 22:115–143.
- Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: Do folivores really play by different rules? *Evol Anthropol* 16:94–106.

- Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291–309.
- Sterling EJ, Dierenfeld ES, Ashbourne CJ, Feistner ATC. 1994. Dietary intake, food composition and nutrient intake in wild and captive populations of *Daubentonia madagascariensis*. *Folia Primatol* 62:115–124.
- Stone L, Roberts A. 1990. The checkerboard score and species distributions. *Oecologia* 85:74–79.
- Struhsaker T. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers D, Herbert J, editors. *Recent advances in primatology, Vol 1: behaviour*. New York: Academic Press. p 225–248.
- Terborgh J. 1983. *Five New World primates: a study in comparative ecology*. Princeton: Princeton University Press.
- van Roosmalen MGM. 1984. Subcategorizing foods in primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. *Food acquisition and processing in primates*. Chicago: Plenum Press. p 167–176.
- van Schaik CP, van Hooff J. 1983. On the ultimate causes of primate social systems. *Behavior* 85:91–117.
- Vasey N. 2003. *Varecia*, ruffed lemurs. In: Goodman SM, Benstead JP, editors. *The natural history of Madagascar*. Chicago: University of Chicago Press. p 1332–1336.
- Walker EP. 1975. *Mammals of the world*. Baltimore: Johns Hopkins University Press.
- Wilson JB. 1995. Null models for assembly rules: the Jack Horner effect is more insidious than the narcissus effect. *Oikos* 72:139–144.
- Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32:199–209.