

# Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest among distantly related species

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**Abstract** Assessing the importance of deterministic processes in structuring ecological communities is a central focus of community ecology. Typically, community ecologists study a single taxonomic group, which precludes detection of potentially important biotic interactions between distantly related species, and inherently assumes competition is strongest between closely related species. We examined distribution patterns of vertebrate species across the island of Borneo in Southeast Asia to assess the extent to which inter-specific competition may have shaped ecological communities on the island and whether the intensity of inter-specific competition in present-day

communities varies as a function of evolutionary relatedness. We investigated the relative extent of competition within and between species of primates, birds, bats and squirrels using species presence–absence and attribute data compiled for 21 forested sites across Borneo. We calculated for each species pair the checkerboard unit value (CU), a statistic that is often interpreted as indicating the importance of interspecific competition. The percentage of species pairs with significant CUs was lowest in within-taxon comparisons. Moreover, for invertebrate-eating species the percentage of significantly checkerboarded species pairs was highest in comparisons between primates and other taxa, particularly birds and squirrels. Our results are consistent with the interpretation that competitive interactions between distantly related species may have shaped the distribution of species and thus the composition of Bornean vertebrate communities. This research highlights the importance of taking into account the broad

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mammalian and avian communities in which species occur for understanding the factors that structure biodiversity.

**Keywords** Community assembly · Niche differentiation · Interspecific competition · Southeast Asia · Checkerboard

## Introduction

A central focus of community ecology is to identify the underlying processes that explain why some species, and not others, are found in biological communities. Assessing the relative importance of stochasticity and deterministic processes (i.e., ecological rules) in structuring ecological communities is central to this goal. A substantial body of ecological theory and research has explored how interspecific competition can promote niche differentiation as a mechanism enabling species coexistence (Hutchinson 1957; Palmer 1994; Chesson 2000). According to niche theory, individual species are the most abundant under the ecological conditions to which they are best adapted. Competition between species can drive divergences in traits so that each species has a particular set of conditions, or niche, in which it thrives. At the community level, niche differentiation can result in the partitioning of resources among species, making it possible for species to co-occur. On the other hand, a lack of niche differentiation may result in the competitive exclusion of the inferior competitor (Tilman 1982). Evaluating the effects of competition and niche differentiation on communities across spatial scales and in diverse ecological systems is a topic that has attracted considerable attention recently (Finke and Snyder 2008; Levine and Hille Ris Lambers 2009; Gotelli et al. 2010), yet we note that much of this work has been largely focused on taxonomically restricted assemblages.

While a growing body of research has examined factors affecting the structure of tropical communities, most research has focused on plants (Hubbell 1979; Webb and Peart 2000; Condit et al. 2002; Tuomisto et al. 2003). In contrast, we have limited understanding of how tropical faunal communities are assembled. We propose that primates are an excellent taxon for investigating tropical vertebrate community structure because they are a major component of vertebrate biomass in many tropical forests (Terborgh 1983) and relatively easy to survey due to their typically diurnal activity patterns, relatively large bodies, and noisy group-living behavior (Emmons 1999). For these reasons, primates are well studied and also well represented in zoological museum collections, providing many presence records.

Many of the attributes that have led to data availability have also caused primates to be vulnerable to population

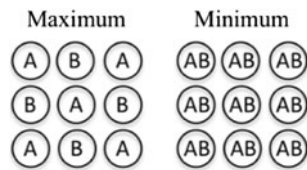
declines from hunting (Wright 2003), suggesting that the composition of current primate communities may differ from that which characterized them for much of their evolutionary history. This has the potential to confound studies attempting to uncover the processes that produced the primate communities that we observe today (Struhsaker 1999). While we agree that it is wise to consider biases that may be introduced by recent hunting and other anthropogenic disturbance, it is likely that hunting has affected the relative abundances of species more than their presence or absence, suggesting that analyses based on distribution, such as that which we present here, are likely to be less affected by such biases.

A great deal of effort has gone into understanding how niche space is divided among primate species by differences in diet, canopy use, habitat use and body size among other parameters (Bourlière 1985; Fleagle et al. 1999; Schreier et al. 2009; Kamilar and Muldoon 2010). In these studies, communities of primates have typically been considered in isolation from the other taxa with which they co-occur. Consequently, primate community ecology has been largely predicated on the assumption that primates compete predominantly with other primate species. However, the full suite of species with which primates compete likely includes non-primate taxa (Strum and Western 1982; Estrada and Coates-Estrada 1985; Ganzhorn 1999; French and Smith 2005; Marshall et al. 2009).

Methodological obstacles, such as obtaining standardized data across taxonomic groups, may have historically limited researchers from examining multiple orders across large spatial scales. Nevertheless, explicitly studying primates in the context of the broader faunal communities in which they occur may shed light on the factors that have affected these communities. Given recent growth in data sharing, the potential benefits of improving our understanding of ecological and evolutionary processes shaping community composition may outweigh logistical challenges in data collection.

We have highlighted the taxon-specific focus in primatology, but more broadly community ecologists and macroecologists often employ a taxon-centered approach, in which studies are restricted to a set of closely related species. We present this paper as a case study to evaluate the potential impact of considering more taxonomically extensive communities. We do this by using a guild approach defined by resource use (Fauth et al. 1996) and focusing on variation across sites in the species composition of local guilds.

Here we examine competitive exclusion between closely and distantly related species. Competitive exclusion can be inferred based on the presence of checkerboard distributions (Diamond 1975), which refers to the distributions of two species that co-occur significantly less often than is



**Fig. 1** Depiction of a maximum and minimum checkerboard distribution of species A and B. Each circle represents a site. In a completely checkerboarded distribution, the two species do not co-occur at any site; in a minimally checkerboarded distribution, the two species consistently co-occur

expected by chance. Checkerboard distributions are observed as the alternating presence of ecologically similar species on islands or other habitat patches (Fig. 1).

We emphasize that our study cannot demonstrate that competition has occurred, but can identify patterns that may have resulted from competitive interactions. Conclusive evidence demonstrating competition would require experimental manipulation (Connell 1980), which would be difficult if not impossible, ethically, to obtain for long-lived, free-ranging and in some cases endangered tropical vertebrates. Thus, significantly high checkerboard unit values (CUs) are consistent with the interpretation that competitive exclusion has shaped the distribution of the species pair under consideration, but mechanisms other than competition, such as habitat and historical effects, can also produce significantly checkerboarded distributions (Gotelli and McCabe 2002). Nevertheless, we evaluate checkerboard distributions at the species-pair level as a starting point for teasing apart the potential effects of competition from the multiple mechanisms that play a role in shaping community composition.

In this study, we investigate the relative intensity of potential competition within and between species of primates, birds, bats and squirrels. For each pair of species included in the study, we determine whether their distributions are significantly checkerboarded. We calculate the percent of significantly checkerboarded species pairs for each taxon comparison (e.g., primate–primate species pairs, primate–bird species pairs). We then define the relative intensity of potential competition as the difference in the percentage of significantly checkerboarded species pairs between taxa. Taxa with more potential competition exhibit a greater percentage of significantly checkerboarded species distributions. We evaluate the percentage of significantly checkerboarded species pairs within and between taxonomic groups to investigate whether patterns consistent with competitive exclusion are more common for closely related pairs of species or for pairs of species that are more distantly related as expressed by their inclusion in higher-level taxonomic classifications.

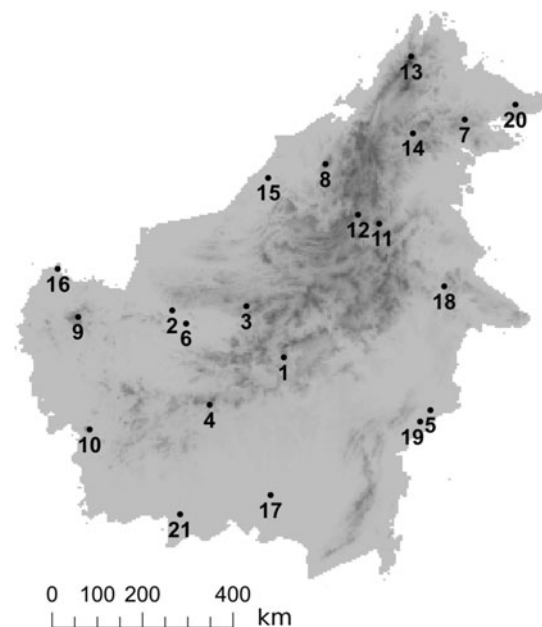
## Materials and methods

### Data compilation

We focus on the island of Borneo to investigate the extent of interspecific competition within and between vertebrate taxa. We use the non-specific term “taxa” because we compare pairs of species between orders (Primates, Chiroptera, Rodentia) and classes (Aves, Mammalia).

Previous research has suggested that interspecific competition between primates and other taxa is likely strong on Borneo (Ganzhorn 1999; Beaudrot et al. 2013). Bornean primate communities are peculiar because of their low species richness in comparison with primate communities in other regions (Bourlière 1985); they do not exhibit the positive relationship between primate species richness and rainfall found in other regions (Reed and Fleagle 1995). In addition, Ganzhorn (1999) suggested that competition between Bornean primates might be lower than that of primates in other regions, and that these primates may be competing more extensively with non-primates based on his finding that Bornean primates exhibited much lower primate body mass ratios than primates in other regions.

We compiled species presence–absence data on bats, birds, primates and squirrels from a combination of published and unpublished sources (see Appendix S1 in Supplementary Information) for 21 forested sites located throughout Borneo (Fig. 2). The sites represent all major



**Fig. 2** Locations of sites on Borneo in Southeast Asia. Elevation is shown in gray with higher elevation indicated by darker shading. Data are projected using geographic coordinate system WGS 1984

**Table 1** Bornean sites

ID	Site	Habitats	Area (km <sup>2</sup> )
1	Barito Ulu	L	4.3
2	Batang Ai National Park	H, U	1,688
3	Betung Kerihun National Park <sup>a</sup>	H, L, U	8,000
4	Bukit Raya-Bukit Baka National Park <sup>a</sup>	H, L, U	1,810
5	Bukit Soeharto Wildlife Reserve	H, L	618
6	Danau Sentarum National Park	S	800
7	Danum Valley Conservation Forest	H, L	427
8	Gunung Mulu National Park	K	528
9	Gunung Niut Wildlife Reserve	H, U	1,800
10	Gunung Palung National Park	H, L, M, S	900
11	Inhutani Logging Concession	H, L	390
12	Kayan Mentarang National Park <sup>a</sup>	H, L, U	16,000
13	Kinabalu National Park <sup>a</sup>	H, L, U	754
14	Maliau Basin Conservation Area <sup>a</sup>	H, L, U	390
15	Niah National Park	K	31
16	Samunsam Wildlife Sanctuary	L, M, S	61
17	Sebangau National Park	S	5,678
18	Sungai Lesan Protection Forest <sup>a</sup>	H, L, U	120
19	Sungai Wain Protection Forest	L	100
20	Tabin Wildlife Reserve	L	1,120
21	Tanjung Puting National Park	L, M, S	3,550

Identity (ID) numbers correspond with locations in Fig. 2. Habitat types include mangrove (M), peat or riverine swamp forest (S), lowland dipterocarp or heath forest (L), hill dipterocarp forest (H), montane forest (U) and karst forest (K) following published categorizations (Struebig et al. 2010)

<sup>a</sup> Inclusion in the checkerboard analysis controlling for habitat types

habitat types found on Borneo, including mangrove, swamp, lowland, hill, montane and karst forests (Table 1).

We focused on species with the greatest potential overlap in diet and canopy use with primates because we were interested in the effects of species competing with primates for food. We therefore make the assumption that dietary overlap provides the opportunity for interspecific competition but we note that there has been extensive debate about this assumption (Schoener 1982).

Given that primates feed almost exclusively in the forest canopy, we included only arboreal and volant species. We excluded carnivorous species but included insectivores because the only carnivorous Bornean primate species is the tarsier, which feeds predominately on insects. In addition, we excluded small, non-volant mammals because distribution data for many species (e.g., rats and shrews) are very limited and cryptic species at many sites are likely overlooked. For similar reasons we also excluded bat species within the families Molossididae and Emballonuridae, and vespertilionid sub-families Miniopterinae and

**Table 2** Number of species included in analyses

	Primates	Birds	Bats	Squirrels
All sites ( <i>n</i> = 21)				
Fruits	7	88	15	9
Invertebrates	4	179	34	7
Habitat sites ( <i>n</i> = 6)				
Fruits	7	86	12	9
Invertebrates	4	172	26	7
Body size <sup>a</sup>				
	8	8	1	4

<sup>a</sup> More than 0.5 kg and less than 10 kg

Vespertilioninae, thus focusing on fruit bats and forest specialist bat species (sensu Struebig et al. 2010) that are better sampled over Borneo. As a result, our study included primate, squirrel and bat species that together comprise nearly 50 % of all non-marine Bornean mammal species. In addition, we included resident birds that forage in the canopy because there is evidence of considerable dietary overlap between some frugivorous birds and primates in Borneo (Leighton and Leighton 1983; Marshall et al. 2009) and other regions (Gautier-Hion et al. 1980; French and Smith 2005).

We used published descriptions to classify each species based on arboreality (terrestrial or non-terrestrial), resident status (resident or non-resident), and diet (Payne et al. 1985; MacKinnon et al. 1993; Fleagle et al. 1999; Myers 2009). We defined arboreal species as aerial foragers and those that feed in lower, middle or upper story of the forest canopy, but not those that feed on the forest floor. We considered all bat, primate and squirrel species as residents and used published data to classify bird resident status (Mann 2008). We used broad dietary categories to code for the presence or absence of items (e.g., invertebrates, fruits) in the diet of each species based on qualitative diet descriptions. Lastly, we compiled data on body size for each species (Payne et al. 1985; Dunning 2008; Jones et al. 2009). The number of species included in each analysis is summarized in Table 2. See Appendix S2 in Supplementary Information for lists of species included in each analysis.

## Analyses

Traditional community-level co-occurrence approaches analyze the entire presence–absence matrix of community data, which consists of species as rows and sites as columns. However, methodological developments have revealed that community-level analyses of presence–absence data are unable to differentiate between multiple co-occurrence patterns, including segregated, aggregated or nested distributions, which provides the impetus for

species-pair analyses because different mechanisms are believed to produce these different distributions (Ulrich and Gotelli 2012). For example, if competition between a pair of species results in competitive exclusion, then a pair of species will not co-occur and therefore competition can cause a segregated distribution. On the other hand, positive interspecific interactions may result in aggregated distributions in which pairs of species consistently co-occur. A number of recent studies have therefore investigated co-occurrence patterns at the species-pair level rather than at the level of the entire community (Sfenthourakis et al. 2005; Sanderson et al. 2009; Cardillo and Meijaard 2010). The species-pair approach restricts the level of analysis to two species and evaluates distribution patterns for each pair without then averaging the species-pair values across the whole community, as was done by early analyses.

We identified species pairs with significantly high CUs. At least two programs, PAIRS and COOC, have been developed to investigate CUs at the species-pair level. We chose to adapt the *oecosimu* function in the *vegan* package in R (R Development Core Team 2012; Oksanen et al. 2013) rather than use pre-existing software for the following reasons: the program PAIRS conducts similar analyses but is limited to a maximum of 150 species (Ulrich 2008), which is less than the number of species included in some of our analyses; the program COOC uses only 5,000 simulations (Sfenthourakis et al. 2004), which can result in high type I error rates when large numbers of species are included (Fayle and Manica 2010).

To identify significantly checkerboarded species pairs, we created a null distribution based on 10,000 simulations. For each simulation, we calculated the CU of each species pair  $i$  and  $j$ :  $CU_{ij} = (r_i - S_{ij})(r_j - S_{ij})$ , where  $r_i$  and  $r_j$  are the total number of occurrences across sites of species  $i$  and  $j$  and  $S$  is the number of sites where the two species co-occur (Stone and Roberts 1990). We used the *tswap* method to create simulated communities so that all possible results were produced with equal chance (Miklos and Podani 2004). This method retained both row and column totals. We used 30,000 trial swaps to generate the initial null model. To moderate the increased likelihood of type I errors as matrix size increased, we used the same number of trial swaps between each successive null model as the number of species pairs in the matrix. Using the simulated data, we calculated the probability density function for each species pair and compared the observed CU to the values expected under the null distribution. We considered a species pair to be significantly checkerboarded if its observed CU was in the top 5 % of its simulated null distribution (see Appendix S3 in Supplementary Information).

To summarize, we determined whether a species pair was significantly checkerboarded by comparing its

observed checkerboard value to a distribution of simulated values. If an observed value was in the highest 5 % of simulated values, we considered the observed value to have been unlikely to have occurred by chance and thus classified the species pair as significantly checkerboarded. We then determined the percentage of significant species pairs in each broader taxonomic comparison (e.g., primate–primate, primate–bird, primate–bat) by dividing the number of significant species pairs by the number of possible species pairs for that taxonomic comparison. We compare the relative intensity of potential competition based on differences in the percentages of significantly checkerboarded species pairs.

We note that using the top 5 % of the distribution does not control for family-wise error rate arising from multiple tests. However, even the most checkerboarded species pair, which was known to consist of two allopatric gibbon species, failed to meet the probability cut-off necessary to satisfy a Bonferroni correction of any kind (Benjamini and Hochberg 1995). We therefore concluded that a Bonferroni correction is too stringent and we instead exercise caution in the interpretation of results (Moran 2003; Nakagawa 2004). Because of the likelihood of obtaining false-positive results, we reduced the number of species included in the analyses using species traits (i.e., arboreality, resident status and diet) to target potentially interacting species (Gotelli and Ulrich 2010).

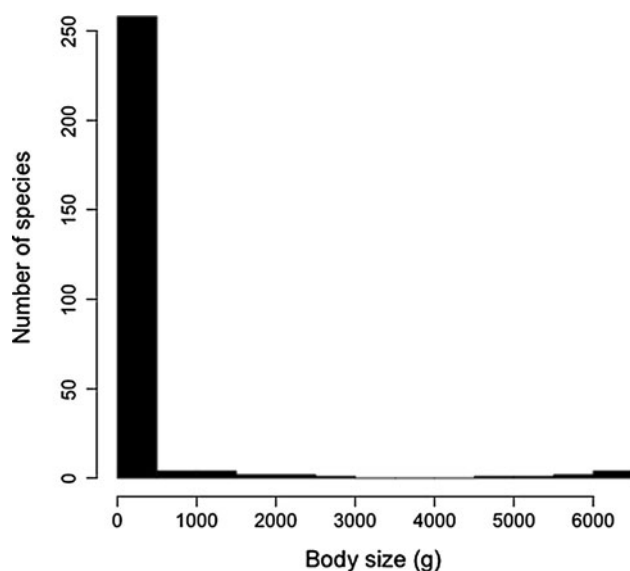
Previous studies have noted the potential for variation in habitats to produce significant checkerboard patterns that are the result of species responding to their preferred habitat rather than competing with other species (Gotelli and McCabe 2002; Gotelli et al. 2010). We therefore conducted additional analyses with a subset of the sites that contained the same major habitat types of lowland, hill and montane forest to control for at least the macro-level effects of habitat (Table 1).

Lastly, we conducted an analysis to assess the extent to which species pairs were checkerboarded using species of similar body sizes. For this analysis, we began with all arboreal, resident species. We excluded two outlier species that were much heavier than 10 kg (*Pongo pygmaeus* and *Nasalis larvatus*). Of the remaining species, most were concentrated in the small body range (i.e., <0.5 kg) (Fig. 3). We included the remaining 21 species with body sizes greater than 0.5 kg to examine distribution patterns of species with medium body sizes (Table 2).

## Results

When all sites ( $n = 21$ ) were included in analyses, the overall percentage of significantly checkerboarded species pairs was 3.4 % of 24,976 species pairs for species with





**Fig. 3** Histogram of species' body sizes. Histogram excludes two outliers with body sizes >10 kg (*Pongo pygmaeus* and *Nasalis larvatus*). Most species in the dataset weighed less than 0.5 kg. Species-pair checkerboard analysis of 21 medium-sized species (0.5–10 kg) at sites with similar habitat ( $n = 6$ ) did not reveal any significantly checkerboarded species pairs

invertebrates in their diet and 3.1 % of 7,021 species pairs for species with fruits in their diet. When only sites with similar habitat types ( $n = 6$ ) were included in the analyses, the overall percentage of significantly checkerboarded species pairs was 0.9 % of 21,736 species pairs for species with invertebrates in their diet and 0.3 % of 6,441 species pairs for species with fruits in their diet.

For species with invertebrates in their diet and using data from all sites, the percentage of significantly checkerboarded species pairs in the within-taxon comparisons was: squirrel–squirrel = 0 %, primate–primate = 0 %, bat–bat = 0.02 %, bird–bird 0.02 %. In the between-higher-level taxa comparisons, the percentage of significantly checkerboarded species pairs was: bird–bat 0.04 %, primate–bat 0.05 %, bird–squirrel 0.09 %, bat–squirrel 0.14 %, primate–bird 0.11 %, primate–squirrel 0.25 % (Table 3).

For species with fruit in their diet and using data from all sites, the percentage of significantly checkerboarded species pairs in the within-taxon comparisons was: squirrel–squirrel = 0 %, primate–primate = 0.05 %, bat–bat = 0 %, bird–bird 0.01 %. For the between-higher-level taxa comparisons, the percent of significantly checkerboarded species pairs was: bird–bat 0.05 %, primate–bat 0.01 %, bird–squirrel 0.05 %, bat–squirrel 0.05 %, primate–bird 0.06 %, primate–squirrel 0.06 % (Table 3).

For species with invertebrates in their diet and restricting analysis to sites with similar habitats, the percentage of significantly checkerboarded species pairs in the within-

taxon comparisons was: squirrel–squirrel = 0 %, primate–primate = 0 %, bat–bat = 0 %, bird–bird 0.01 %. In the between-higher-level taxa comparisons, the percentage of significantly checkerboarded species pairs was: bird–bat 0.01 %, primate–bat 0.01 %, bird–squirrel 0.01 %, bat–squirrel 0.01 %, primate–bird 0.05 %, primate–squirrel 0.07 % (Table 3).

For species with fruits in their diet and restricting analysis to sites with similar habitats, the percentage of significantly checkerboarded species pairs in the within-taxon comparisons was: squirrel–squirrel = 0 %, primate–primate = 0 %, bat–bat = 0 %, bird–bird 0 %. For the between-higher-level taxa comparisons, the percent of significantly checkerboarded species pairs was: bird–bat 0.01 %, primate–bat 0 %, bird–squirrel 0 %, bat–squirrel 0 %, primate–bird 0.01 %, primate–squirrel 0 % (Table 3).

Lastly, the analysis of medium-sized species did not reveal any significantly checkerboarded species pairs.

## Discussion

The goal of our study was to identify patterns of species distributions and in doing so to evaluate the relative extent of potential competition within and between species of primates, birds, bats and squirrels in forested areas across Borneo. We tested for patterns consistent with competitive exclusion determining the presence or absence of species in these communities. We modified the classic community-level checkerboard approach to evaluate significantly checkerboarded species pairs and calculated the percentage of significantly checkerboarded species pairs within and between taxonomic groups, which can be interpreted as the result of competitive exclusion structuring the distribution of species pairs.

Overall, significantly checkerboarded species pairs were uncommon, which suggests that competition to the extent of competitive exclusion is rare. However, of the significantly checkerboarded species pairs, the percentages were consistently lower for closely related species pairs than for distantly related species pairs. We interpret this to signify that rates of competitive exclusion are lowest among species of the same class (Aves) or order (Chiroptera, Primates, Rodentia). Moreover, among invertebrate-eating species, the highest values were between primates and distantly related taxa, particularly birds and squirrels, which may indicate that the rates of competitive exclusion are highest between primates and other vertebrates. The overall patterns persisted after controlling for variation in habitat types. Moreover, results from this study at the species-pair level are consistent with results from community-wide analyses of the same dataset (Beaudrot et al. 2013).

**Table 3** Percent of significantly checkerboarded species pairs for invertebrate-eating species in all sites (*Invertebrate/all sites*;  $n = 21$ ), fruit-eating species in all sites (*Fruit/all sites*;  $n = 21$ ), invertebrate-eating species in sites with similar habitat (*Invertebrate/similar habitat*;  $n = 6$ ), fruit-eating species in sites with similar habitat (*Fruit/similar habitat*;  $n = 6$ )

Invertebrate/all sites	Primate	Bat	Bird	Squirrel	Fruit/all sites	Primate	Bat	Bird	Squirrel
Primate	0.00 <sup>a</sup>	0.05 <sup>b</sup>	0.11 <sup>b</sup>	0.25 <sup>b</sup>	Primate	0.05 <sup>a</sup>	0.10 <sup>b</sup>	0.06 <sup>b</sup>	0.06 <sup>b</sup>
Bat	0.05	0.02 <sup>a</sup>	0.04	0.14	Bat	0.10	0.00 <sup>a</sup>	0.05	0.05
Bird	0.11	0.04	0.02 <sup>a</sup>	0.09	Bird	0.06	0.05	0.01 <sup>a</sup>	0.05
Squirrel	0.25	0.02	0.09	0.00 <sup>a</sup>	Squirrel	0.06	0.01	0.05	0.00 <sup>a</sup>
Invertebrate/similar habitat	Primate	Bat	Bird	Squirrel	Fruit/similar habitat	Primate	Bat	Bird	Squirrel
Primate	0.00 <sup>a</sup>	0.01	0.05 <sup>b</sup>	0.07 <sup>b</sup>	Primate	0.00 <sup>a</sup>	0.00	0.01 <sup>b</sup>	0.00
Bat	0.01	0.00 <sup>a</sup>	0.01	0.01	Bat	0.00	0.00 <sup>a</sup>	0.01	0.00
Bird	0.05	0.01	0.01 <sup>a</sup>	0.01	Bird	0.01	0.01	0.00 <sup>a</sup>	0.00
Squirrel	0.07	0.01	0.01	0.00 <sup>a</sup>	Squirrel	0.00	0.00	0.00	0.00 <sup>a</sup>

The percent of species pairs with significant checkerboard unit values was lowest in within-taxon comparisons. The percent of significantly checkerboarded species pairs was high in comparisons between primates and other taxa, particularly birds and squirrels. We interpret the difference in the percentage of significantly checkerboarded species pairs in a comparison of two taxa as the relative intensity of competition within and between taxa

<sup>a</sup> Lowest column values

<sup>b</sup> Highest column values

A dominant finding from our analyses was that rates of competitive exclusion between Bornean vertebrates appear to be quite low. A number of factors other than competitive biotic interactions likely affect species distributions in these forests, including palaeogeography and palaeoenvironment, evolutionary history, dispersal limitation and the current environmental conditions (Kamilar 2009; Slik et al. 2011). We highlight, however, that detecting significant checkerboard scores from presence–absence data suggests that the most extreme form of competition (i.e., competitive exclusion) occurs in these communities. We suggest that these results also raise the question of how competition between distantly related species affects community composition in less extreme forms. For example, how does interspecific competition affect the relative abundances of species pairs that do not exhibit checkerboard distributions?

#### Limitations and alternative explanations

Although the data in this study represent the best available information on Bornean vertebrates, data on rare species are nonetheless limited. Sampling effort was not standardized across sites because we compiled data rather than conducting systematic surveys at all sites. While it is inevitable that there may be variation in detection across taxonomic groups, we minimized the effect of this by focusing on sites and vertebrate groups that are relatively well surveyed. We highlight that for biogeographical studies, data compilation methods like ours are often employed (Cardillo and Meijaard 2010; Kamilar and Ledogar 2011), but we recommend future work investigate the potential for species–area

relationships and variation in sampling effort to affect co-occurrence patterns. We also suggest that future work incorporate the influence of hunting pressure on local extinction (Meijaard and Nijman 2000; Nijman 2004; Meijaard et al. 2011) and how this may affect co-occurrence patterns. We note that there has been recent debate over the extent to which variation among species' geographic ranges due to historical biogeography and dispersal limitation may drive checkerboard distributions (Collins et al. 2011; Sanderson et al. 2011). Historical effects, such as long-term changes in vegetation cover or past hunting may have also shaped present-day species distributions and thus must be considered a potential mechanism for producing checkerboard patterns. We have not taken historical changes in forest cover into account, but suggest future studies test this explicitly using historical vegetation reconstructions (Bird et al. 2005; Slik et al. 2011). Moreover these mechanisms are not necessarily mutually exclusive and may have operated in addition to other factors that affect species distributions. Lastly, our study explicitly assumes that current community composition is in part due to competition between species that has occurred in the past. Because we are simply investigating a “snapshot” of current community composition, we are unable to evaluate long-term community dynamics and how interactions between species may have affected community composition over evolutionary time. For example, the absence of checkerboard distributions could have occurred as the product of two species having not competed in the past but could also have occurred if two species had competed extensively in the past to the point that niche differentiation resulted.

Because we did not control for family-wise error rate (see “[Materials and methods](#)”), it is possible that any and all significantly checkerboarded species-pairs may be false-positives. Based on an  $\alpha$ -value of 0.05, we might expect 5 % of species pairs to exhibit significant checkerboard distributions as the result of statistical error even if the null hypothesis were true. The observed percentage of significantly checkerboarded species pairs was less than 5 % in all analyses. However, if our null model were truly a null model, there is no reason to expect systematic patterning in the results. We therefore interpret the consistent patterning across tests as evidence of biologically meaningful deviation from the null model. We do, however, avoid making inferences about individual species pairs on biological grounds because of the likelihood of having obtained false-positives.

Variation in habitats across sites might serve as a possible alternative explanation for the results of this study. It has previously been documented that habitat checkerboards can produce patterns of species checkerboards (Gotelli and McCabe 2002). The reduction in the percentage of significantly checkerboarded species pairs following re-analysis based on sites with similar habitat suggests that habitat checkerboards may have driven the higher rates of significantly checkerboarded species pairs found when all sites were considered. While it is possible that additional habitat variation was unaccounted for, we interpret the patterns as consistent with interspecific competition. Community-level analyses of the same dataset using the software EcoSim also found consistent patterns before and after controlling for habitat effects (Beaudrot et al. 2013).

### Competition strength

These findings raise the question of why competitive exclusion appears lower in comparisons of species within the same taxonomic group than in comparisons between higher-level groups, particularly because biologists have classically argued that competition should be most intense between closely related species (Darwin 1859; Elton and Miller 1954). Cahill et al. (2008) termed this the “competition-relatedness hypothesis” and highlighted that while it is a common assumption in evolutionary biology it has rarely been tested. Moreover, Cahill et al. (2008) found no support for it in their analysis of vascular plants; like our study, their results were consistent with the hypothesis that competition was stronger between more distantly related species. Furthermore, Mayfield and Levine (2010) have suggested that irrespective of phylogenetic relatedness, competitive exclusion occurs when differences in competitive ability between species exceed niche differences. It is also possible that the results we found are due to past

competition having driven differentiation between closely related species thus enabling co-existence (e.g., sufficient divergence from past competition among species of similar body size may be the reason why the analysis of medium-sized species did not produce any significantly checkerboarded species pairs). Additional tests of the competition-relatedness hypothesis and framework may provide further insight into the roles of past and present competition in this system.

Our findings also raise the question of why competitive exclusion appears strongest between invertebrate-eating primates and other taxa. One possible cause for greater evidence of competitive exclusion in invertebrate-eating species is because most primate species that consume invertebrates are relatively small (Clutton-Brock and Harvey 1977). Smaller primates are more similar in body size to many of the non-primate taxa in our data set than they are to the other primate species, which may contribute to the strength of competition between these small primates and similar-sized non-primates. Additionally, larger bodied species may be buffered through periods of low food availability because of their slower metabolic rate, increased fat reserves, or ability to switch to abundant, low quality foods during periods of food scarcity. Smaller bodied species with high metabolic rates may be subject to more detrimental effects from exploitative competition for invertebrates and consequently may exhibit stronger checkerboard distributions with larger species.

We focused on Borneo because we expected competition between primates and other taxa to be particularly strong in this region. Whether our results can be generalized to other biogeographic regions remains an open question and we encourage others to evaluate the relative extent of competition within and between taxa elsewhere. Recent biogeographic comparisons have examined primates without consideration of other orders. These studies have suggested that competition is an important factor that influences primate communities in Madagascar (Razafindratsima et al. 2012), but not in the other major regions in which primates occur, which include the Neotropics, Africa and Asia (Kamilar and Guidi 2010; Beaudrot and Marshall 2011). This difference may be because primates make up a larger percentage of the mammalian community in Madagascar than in other regions (Thalmann 2007). Primate species may consequently be competing with other primate species more in Madagascar than in other regions where they may be competing with non-primate species (Beaudrot and Marshall 2011). Other parts of Southeast Asia, Africa (but not Madagascar) and the Neotropics thus provide candidate regions for further examination of competition between primates and evolutionarily distant species.



## Conclusion

This study has demonstrated the presence of significant ecological structure among pairs of Bornean vertebrate species that are evolutionarily quite divergent yet ecologically similar in their resource use. Results are consistent with the interpretation that competitive interactions between species may have shaped the composition of Bornean vertebrate communities through competitive exclusion. Surprisingly, our results suggest that competitive-exclusion patterns were most common among distantly related species pairs. Moreover, competitive-exclusion patterns among invertebrate-eating species pairs were strongest between primates and other taxa, particularly birds and squirrels. This research highlights the importance of considering the broader mammalian and avian communities in which these species occur and contributes to our understanding of the role of deterministic processes in shaping tropical faunal communities. Although we have drawn attention to the restricted taxonomic focus in most of the primate ecology literature, this bias is pervasive throughout studies of many organismal groups. We believe that expanding the study of biotic interactions to include distantly related taxa is an important future area of research in community ecology and macroecology and is a subject that warrants further research across ecological systems.

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