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Abstract. Medium- and large-sized vertebrates play a key role in shaping overall forest functioning. Despite this, vertebrate interactions, from competition to mutualism, remain poorly studied, even though these interactions should be taken into account in our conservation and management strategies. Thus, we tackled the question of vertebrate co-occurrence in tropical rainforests: Are (negative or positive) co-occurrences dependent on forest structure and composition? and Are these co-occurrences linked to functional species similarity? We recorded the occurrence of 21 medium- and large-sized vertebrates in 19 French Guianan locations in which a large set of forest structure and composition descriptors were collected. We used a probabilistic model to look for co-occurrences at different spatial scales, and species pairwise co-occurrences were then compared to those generated solely on the basis of forest structure and composition. We then quantified the co-occurrence strength between pairwise species dyads and determined whether they relied on species functional similarity, controlling for the environmental effects. We found that positive co-occurrences vastly outnumbered negative co-occurrences, were only partly shaped by the local environment, and were closely linked to species functional similarity. Thus, groups of species sharing similar functional traits are more prone to co-occur, highlighting the key role of functional redundancy in structuring species assemblages. We discuss how positive interactions could generate the predominance of positive co-occurrences in oligotrophic *terra firme* (unflooded) forests when resources are scarce and dispersed in dry season. Finally, we identified functional groups based on co-occurrence strength and suggested that frugivory/granivory and body size are of primary importance in species interactions in Neotropical vertebrate communities.

Key words: activity matching; birds; Guiana Shield; information exchange; mammals; mixed-species associations; mutualism; *terra firme* rainforests.

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INTRODUCTION

Deciphering the underlying ecological reasons for species co-occurrence in space and time is a delicate issue, as co-occurrence depends on both the species' environmental requirements and the interspecific interactions within a community (Peres-Neto 2004, Sfenthourakis et al. 2006). In

fact, when the environmental requirements (the so-called fundamental niche) of two species become increasingly similar, the chance of co-occurrence is obviously increased. But, the presence of (negative or positive) interspecific interactions modifies the range of habitat within which each species lives, that is, their ecological (or realized) niche (Bruno et al. 2003). First, the interspecific interactions modify how the available resources (e.g., water, food, shelter) can be exploited and shared by the two species, and, second, how they can physiologically resist the environmental conditions (non-resource-related conditions such as heat, cold, wind, salinity, or soil structure) (Maestre et al. 2009). Depending on the interspecific interactions involved between two given species, one or these two species can derive benefit or costs from the interaction that may change co-occurrence patterns with respect to resources and environmental conditions.

Interspecific interaction processes remain poorly studied in tropical rainforests and within medium- and large-sized vertebrate communities, with the exception of vertebrate assemblages in African savannas (Skogland 1991, Arsenault and Owen-Smith 2002, du Toit 2003, Odadi et al. 2011, Périquet et al. 2015). Negative interactions are often considered to play a major role in determining local patterns of species co-occurrence, the most widely studied being competition for resources and predation. Conversely, positive interspecific interactions are often under-estimated or neglected (Dickman 1992, Stachowicz 2001). However, there are numerous examples showing that the presence of a species may directly help another species to establish and/or persist (Stachowicz 2001, Kraft et al. 2015) by habitat amelioration, resource enhancement, predation reduction, pollination enhancement, and so on (Bruno et al. 2003, Valiente-Banuet and Verdú 2007). Positive interaction processes are, indeed, widely demonstrated in studies of plant–pollinator, plant–fungi, and plant–bacteria interactions.

The development of functional trait-based approaches in community ecology has provided valuable insights into the ecological processes that determine species co-occurrence. Functional trait-based approaches have advantages over those that use phylogeny in separating different components of species niche. Basically, the more functionally similar the species are, the more

they should share similar environmental requirements and use similar resources, and thus, the more they should compete, that is, have negative interactions. If two species are strictly functionally similar, we expect a symmetrical competition between them. Because of this, congeneric species, under the hypothesis of phylogenetic conservatism of functional traits, should be engaged in a battle for resources (Sfenthourakis et al. 2006) so that resource partitioning can be viewed as an ecological mechanism that reduces the cost of competition: Similar (or congeneric) species in the scenario would either use a common resource in different places or in different time. On the other hand, studies which have examined positive co-occurrences from a functional point of view tend to show interspecific complementarity (functionally dissimilar species) in functional space (Valiente-Banuet and Verdú 2007). However, mixed-species associations of functionally similar animal species could provide some advantages via an increase in the number of individuals in the association (predation reduction, resource enhancement, ...) while limiting intraspecific competition (Terborgh 1990).

Neotropical rainforests have been considered as the most species-rich forests worldwide. Guianan forests are however characterized by lower diversity when compared to western Amazonia, in both plants and mammals (Voss and Emmons [1996], Ter Steege et al. [2000], and references therein). The *terra firme* (i.e., unflooded) rainforests that dominate the Guianan region are characterized by high variability in forest structure (e.g., canopy height, understory density) and tree composition (Guitet et al. 2015*a*). Despite this well-known habitat heterogeneity, large and important environmental descriptors, such as forest landscapes (differentiated by their geomorphological and botanical characteristics), are known to weakly influence medium- and large-sized vertebrate assemblages (Guitet et al. 2015*b*, Richard-Hansen et al. 2015, Denis et al. 2018). The lack of a large-scale pattern may hide true interactions that operate at a finer spatial scales, given that medium- and large-sized vertebrates are very mobile with relatively large home ranges (HRs; generally from a few to several hundreds of ha) but could be highly selective in their micro-habitats within their HR (Arteaga and Vintincinque 2008, Palminteri and Peres 2012,

Luna-Maira et al. 2013). While plant–vertebrate interactions, which play an important role in maintaining forest biomass and tree biodiversity global spatial patterns, have been largely investigated (see Forget et al. [2000]; Peres et al. [2016]; Tabarelli and Peres [2002] for the Neotropics), the interactions within vertebrate assemblages at local scales remain poorly studied. Nevertheless, the majority of studies suggest that vertebrate communities are strongly shaped by interspecific competition (e.g., see Steen et al. [2014] for snakes, Beaudrot et al. [2013] for primates, and Varzinczak et al. [2016] for bats). However, some examples highlight the role of positive interspecific interactions. For example, in Costa Rica, the collared peccaries (*Pecari tajacu*) alter the physical structure of the standing leaf litter that positively influences the abundance of terrestrial amphibians and reptiles (Reider et al. 2013, Ringler et al. 2015). Among grazing herbivores, monkeys, or birds, mixed-species associations provide plenty of advantages, such as reduced predation risk or improved efficiency of space exploration for accessing food or other resources (Terborgh 1990, Dickman 1992, Arsenault and Owen-Smith 2002, Stensland et al. 2003).

In this study, we asked three main questions: (1) What are the predominant co-occurrence types (negative, positive, or random) among medium- and large-sized vertebrate assemblages of the Guianan *terra firme* rainforests? (2) What proportion of these co-occurrences is, on the one hand, dependent on environmental conditions and, on the other hand, dependent on interspecific interactions? (3) Are these co-occurrences linked to functional similarity among medium- and large-sized vertebrates, and if so, which traits are important? And finally, we draw a general scheme of species interactions in the large animal communities of the Guiana Shield Neotropical forests.

MATERIALS AND METHODS

Study area

French Guiana covers ~85,000 km^2 in the eastern part of the Guiana Shield between Suriname and the Brazilian state of Amapa (2°7′–5°44′ N and 51°38′–54°35′ W). Altitude generally ranges between 0 and 200 m above sea level (mean 140 m) with a few peaks above 800 m. The climate is equatorial with annual rainfall ranging from 3600 mm in the northeast to 2000 mm in the south and the west, with a mean annual temperature of about 26°C. The number of consecutive months with <100 mm of precipitation varies from two in the north to three in the south, with high inter-annual variations (Wagner et al. 2011). The geological landform is a 2.2–1.9 Gyr old crystalline basement, which makes up the oldest and most homogeneous part of the Guiana Shield (Delor et al. 2003). Evergreen rainforest covers more than 90% of the inland territory. All sites are located in *terra firme* rainforests distributed across French Guiana (right part of Fig. 1) and are either located within territory under strict protection laws or far enough (at least 6 km on foot) from human activities to be considered exempt from hunting pressure, including from indigenous communities.

Sampling

We employed line transect methods to sample 19 sites using visual counts of 33 medium- and large-sized vertebrates (see list of Appendix S1: Table S1). At each site, four radial line transects (exceptionally three) were walked from a central point (left part of Fig. 1). Each transect was divided into 30 100-m units. The observer (CRH, TD, and others) walked the transect and assigned each detected species to the appropriate unit. The observers systematically alternated transect lines on consecutive days to avoid strong observer bias. Each site was surveyed every morning (07:00–11:00) and afternoon (14:30–18:00) during a field session that lasted seven to nine consecutive days (except at one site, which lasted 16 d). A single field session was conducted per site. Only one of the 19 sites was surveyed early in the rain season (January). The others were surveyed during the dry season (i.e., between July 9 and November 25) between 2005 and 2015. All surveys were carried out under clear conditions. When raining, the sampling was suspended and the observer waited until the effects (i.e., strong wind, water dripping from foliage) had completely stopped before restarting.

Environmental conditions and functional traits

All descriptors of forest structure and forest composition were collected using rapid forestry surveys undertaken in ~90–120 0.2-ha
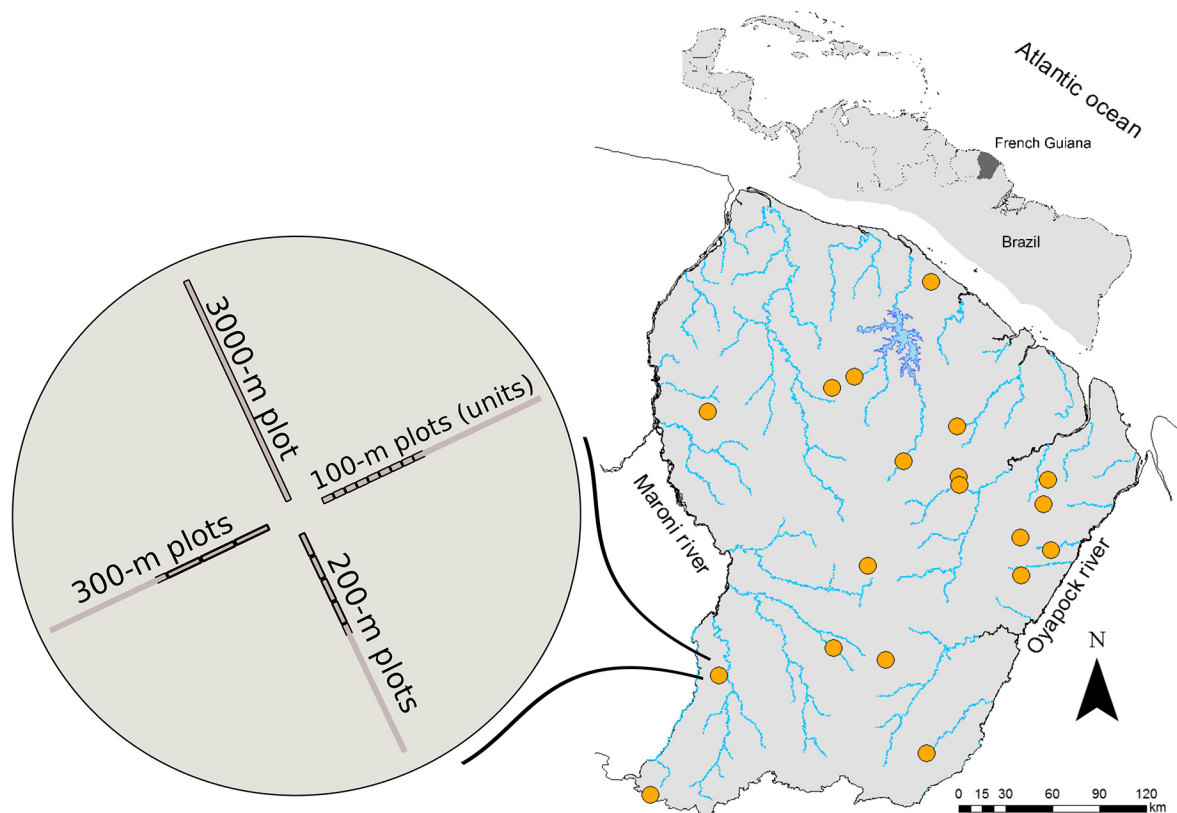
Fig. 1. Study area in French Guiana, northern South America, including 19 survey sites. The left part of the figure illustrates the sampling design: Four line transects were used to sample the diurnal medium- and large-sized vertebrates (100-m transect unit) and environmental conditions (i.e., forest structure and forest composition measured in each plot of 100 m × 20 m). Data were aggregated to calculate species occurrence and environmental conditions for different spatial scales from 200 to 3000 m.

(100 m × 20 m) plots located along line transects. Rapid forest surveys were carried out during the dry season and over a period of 1 month before conducting species counts (Guitet et al. 2015b). The 100-m length plots were grouped together to define 11 plot size classes (to be used in the forthcoming spatial scale analyses), ranging from 200 (two transect units) to 3000 m (30 successive transect units which correspond to one transect).

For forest structure descriptors, we defined 11 variables from field descriptors at all spatial scales (see "forest structure descriptors" in Appendix S1: Table S2). We calculated density of tree species and tree basal area. We calculated tree diameter heterogeneity using the standard deviation of tree diameters. To calculate the density of zoochorous trees, we used a local database

and scientific publications (van Roosmalen 1985a, Ollivier et al. 2007). In the field, we estimated canopy height, canopy openings (importance of canopy gaps), understory density, liana density, understory palm density, and area of tree-fall gaps. Density of *Euterpe* spp. was used to represent interspersing swamp areas.

For forest composition descriptors, all trees and palms with diameter at breast height (1.3 m above the ground) >17.5 cm were measured and floristic determinations were determined using common nomenclature used by foresters in French Guiana (see complete details in Guitet et al. 2014). We then calculated tree taxa abundance variable for all spatial scales (Appendix S1: Table S3).

We identified and described 10 functional traits based on scientific publications from French

Guiana when possible, otherwise from South America (details of functional traits in Table 1). Functional traits were chosen because of their links to resource acquisition, social behavior, and space use of vertebrate species (see Table 1 and references in Denis et al. 2018). Body size (Size), body mass (Mass), mean group size (GrpSize), and size of HR (which are relatively correlated) can summarize how species exploit available resources. For example, largest primates should consume more large seeds and fruits, and largest primates should compete more each other than with smaller primates. Frugivory/granivory (Fruits), herbivory (Veg), and animalivory (Anim) as diet traits can be related to the quality of resources available consumed by functionally similar species. Height of substrate preference (Hgt) can reflect how resource availability and strata (space) are exploited by species. Intraspecific calls and songs (Calls) speak to the importance of intraspecific information exchange. This sociability trait was evaluated based on expert opinions to assess the extent to which different clues help them to detect each species. We used the median value of experts' responses (five experienced observers and/or biologists) for each covariate and each species.

Species co-occurrence

To avoid any bias caused by imperfect detection and false absences (Royan et al. 2016), we chose to remove species which are rarely detected

Table 1. Functional trait covariates of medium- and large-sized vertebrates.

Species	Mass kg	Size m	HR ha	Social –	GrpSize ind/group	Calls –	Hgt –	Fruits %	Veg %	Anim %
Alouatta macconnelli	6.8	0.5	50	3	4.7	1.0	4	58.0	40.0	2.0
Ateles paniscus	8.8	0.4	250	2	2.0	1.0	5	87.0	11.0	2.0
Sapajus apella	3.1	0.3	300	3	14.0	2.0	2	81.0	1.0	18.0
Cebus olivaceus	2.9	0.3	100	3	12.0	1.0	2	53.1	7.4	39.5
Crax alector	3.0	0.7	100	2	2.0	2.0	0	91.2	0.50	8.3
Crypturellus sp.	0.3	0.3	3	1	1.0	0.0	0	89.0	0.0	11.0
Dasyprocta leporina	4.4	0.5	3	1	1.5	0.0	0	87.4	2.3	10.3
Eira barbara	4.8	0.5	2000	1	1.2	0.0	1	21.0	0.0	79.0
Geochelone denticulata	4.4	0.3	30	1	1.0	0.0	0	42.9	29.1	28.0
Mazama americana	36.0	0.8	100	1	1.0	0.0	0	56.0	36.5	7.5
Mazama nemorivaga	14.3	0.7	100	1	1.0	0.0	0	68.30	25.0	6.7
Myoprocta acouchy	1.0	0.3	1	1	1.0	0.0	0	98.5	0.2	1.3
Odontophorus gujanensis	0.3	0.2	5	3	5.6	0.5	0	25.0	25.0	50.0
Pecari tajacu	18.4	0.6	500	3	4.8	0.0	0	64.2	0.0	35.8
Penelope marail	1.0	0.5	30	1	1.8	0.0	2	97.4	0.0	2.6
Pithecia pithecia	2.0	0.3	120	2	3.7	0.0	2	90.3	5.0	4.7
Psophia crepitans	1.1	0.5	100	3	5.8	2.0	0	83.2	0.3	16.6
Saguinus midas	0.5	0.2	50	3	5.7	3.0	1	44.0	0.0	56.0
Saimiri sciureus	0.9	0.3	500	3	20.0	2.5	2	55.1	0.0	44.9
Tapirus terrestris	238.5	1.0	400	1	1.0	0.0	0	24.4	75.5	0.1
Tinamus major	1.0	0.4	5	1	1.0	0.0	0	89.0	0.0	11.0
Median	3.0	0.5	100	2	2.0	0.0	0.0	68.3	1.0	11.0
90% range	0.33–36	0.28–1.25	3–500	1–3	1–14	0–2	0–4	24.4–97.4	0–40	1.3–56

Notes: The unit of measurement is given under each functional trait covariate. Mass: body mass; Size: body size; HR: home range size; Social: social structure (1 = solitary, 2 = family (i.e., a couple with young or subadult individuals) or small subgroups, and 3 = more complex social groups with more than two reproductive adults); GrpSize: mean group size; Calls†: intraspecific calls/songs; Hgt: height of substrate preference (0 = terrestrial species, 1–5 = arboreal species using the lower to upper levels of forests); *Fruits*‡: proportion of frugivory/granivory in the species diet; *Veg*‡: proportion of the herbivory; *Anim*‡: proportion of the animalivory. The median value and the 5% and 95% quantiles (90% range) are given for each functional trait covariate in the two last lines.

† Calls was computed based on expert opinions to assess the extent to which different clues help them to detect each species. We used the median value of experts' responses (five experienced observers and/or biologists) for each species and completed missing data for poorly observed species using a literature search (Denis et al. 2017). We asked them to note the usefulness of cues from 0 (not useful) to 3 (useful in almost all detections).

‡ Find bibliographical references in Denis et al. (2018).

(even though they are present) because species are cryptic (very high sampling effort needed) and/or the sampling design was inadequate (e.g., nocturnal species). We kept species with at least two observations at, at least, three sites to ensure a good degree of confidence in species occurrence (Appendix S1: Table S1). We implemented unconstrained models, which used the observed species presence/absence to compute species co-occurrence. For this, we built a presence/absence matrix of observed species by plot for each spatial scale and used a probabilistic null model to test statistically significant co-occurrences (associations) of pairwise species (Veech 2013). Veech's method (2013) does assume that all plots have the same probability of being occupied by a given species (Arita 2016). This is respected in our data set, since the species are ubiquitous in the whole territory, all plots within a spatial scale have the same size and theoretically the same richness, and sampling effort is relatively homogeneous (see *Sampling* section above). Species co-occurrences were classified as negative, positive, or random from these probabilities at a chosen significance level (*P*). Detection differences exist between species due to their biological traits (Denis et al. 2017, Sólymos et al. 2018). Smaller, solitary, and cryptic species are often less detected than larger, group-living, and non-cryptic species. These biases do not confound the significant co-occurrences of the analysis, but can hide a number of significant co-occurrences for the less detected species during surveys, and thus reduce overall significant co-occurrences.

Co-occurrence dependence on environmental conditions

Environmental conditions were separated into two main components: forest structure and forest composition. First, we performed a principal component analysis (PCA) on the forest structure tables and a non-symmetric correspondence analysis (NSCA) on the forest composition table for each spatial scale to summarize the information contained in the environmental condition tables with a reduced number of dimensions. Principal component analysis produces linear combinations of original covariates to highlight predominant patterns of forest structure. Non-symmetric correspondence analysis seeks to find main patterns of variation in forest composition

change. In contrast to correspondence analysis, NSCA gives a higher weight to most common tree species, which have potentially the strongest effects on vertebrate assemblages. In the subsequent part of the analysis we used, for the forest structure and composition, the plots scores, which are the coordinates of plots on the orthogonal axes in the multi-dimensional space of the ordinations.

We then implemented environmentally constrained models to determine the species co-occurrence as a function of forest structure or composition components (species co-occurrence due to effects of environmental conditions only) (Peres-Neto et al. 2001). For this, we performed a mixed binomial general linear model (GLM) with logit link in which the plot scores of the selected axes were used as fixed effects, and the site as a random factor since plots within a given site were expected to be more similar and should not be considered independent. In the second step, we built the envelope of the expected number of co-occurrence produced by purely environmental effects (from 1000 presence/absence tables predicted by the GLM) using the probabilistic model of Veech (2013). In the last step, we compared the 5th–95th quantile envelope of the two environmentally constrained models (purely environmental effects) with the co-occurrence number generated by the unconstrained model. Doing so, we were able to test whether the species co-occurrence was mediated by the environment or due to true interspecific interactions.

Co-occurrence dependence on traits

To examine how the functional relatedness between species may influence species co-occurrence, we investigated the relationship between the co-occurrence strength ("co-occurrence coefficient") of *unconstrained models* and species functional dissimilarity for each spatial scale. The co-occurrence strength was defined as the difference between the observed and expected number of plots within which the two species i and j co-occur (J_{ij}^{obs}-J_{ij}^{exp}; Veech 2014), and measures both the strength (absolute difference) and the direction (sign) of the co-occurrence. To calculate the trait-based dissimilarity (Euclidean distances), we considered each trait separately as well as species scores on the selected axes after implementing a PCA for all species functional

traits (global species dissimilarities). In order to measure the relationship between co-occurrence strength and species functional dissimilarities, we used a weighted non-parametric correlation coefficient (weighted Spearman's r) with $1/p_{ij}$ as weights, where p_{ij} was the significance level of the co-occurrence of the two species i and j. Thus, the more significant the co-occurrence, the higher the co-occurrence weight. Finally, we compared the observed correlation coefficients with those calculated from the environmentally constrained models to determine whether the relationship between co-occurrence strength and species functional dissimilarity was dependent, or not, on environmental conditions. Significance level was defined as the frequency of observed correlation coefficients outside of those generated by the environmentally constrained models, and was given for the two components of environmental conditions (forest structure and composition).

Defining interacting species groups

Finally, to separate groups within which species mainly interact with each other and identify functional traits that characterized these groups, a hierarchical cluster analysis was performed using in Ward's linkage method from a Jaccard matrix (Jaccard 1901). The Jaccard matrix was generated from a presence/absence matrix of observed species and was chosen to not consider double absences as indications of resemblance. Ward's linkage method seeks to maximize between-groups inertia and minimize within-group inertia. To characterizing the clusters, we compared means of functional traits of each cluster with overall means using a V-test (Cornillon et al. 2012).

Results

Medium- and large-sized vertebrates

Among the 33 surveyed species, 21 were kept in the analysis, including six birds, 14 mammals (seven primates, four Artiodactyla, two Rodentia, and one Carnivora), and one tortoise. Many of them are relatively small, living in small groups, rarely used vocalizations, and had relatively varied diets even though a frugivory/granivory diet was dominant. There was no exclusively carnivorous top predator species (Table 1).

Co-occurrence patterns

We analyzed 210 species pairs. For the unconstrained co-occurrence models, random species co-occurrences dominated the species assemblages. Among the significant co-occurrences, positive co-occurrences were higher than negative co-occurrences, regardless of spatial scale (Appendix S1: Fig. S1 and Fig. 2). The greatest difference between negative and positive co-occurrences (8.5% for $P = 0.05$) occurred in the 600-m plot, with positive co-occurrences more than nine times higher than negative ones. The proportion of negative co-occurrences was statistically not significant and lower than 5% regardless of spatial scale, while the proportion of positive co-occurrences was superior to 5% for the 300- to 1000-m plots with a maximum of 9.5% for the 500- and 600-m plots (Fig. 2).

Effects of environmental conditions on co-occurrence

For the environmentally constrained models, the 5th–95th quantile envelope of the expected number of co-occurrences produced by purely environmental effects was relatively similar for both positive and negative co-occurrences. The 5th–95th quantile envelopes were constant from the 200- to 1000-m plots and slowly decreased after (Fig. 3). The observed number of negative co-occurrences was located almost entirely within the 5th–95th quantile envelope of the both environmentally constrained models (forest structure and composition models) (Fig. 3A). However, the number of negative co-occurrences was so low (<5%; <11 of 210 species pairs) that they could have been generated by random effects, and not by actual environmental conditions. Conversely, a non-negligible number of positive co-occurrences were explained by environmental constraints (part of 5th–95th quantile envelopes >10 species pairs), at all scales considered. Moreover, the observed number of positive co-occurrences was significantly higher than the 5th–95th quantile envelope of the two environmentally constrained models from the 400- to 800-m plots, showing that additive effects occurred at this scale (Fig. 3B). The environmentally constrained model combined forest structure and forest composition covariates showed no additional explanation of co-occurrence number (Appendix S1: Fig. S2). Thus, a large portion
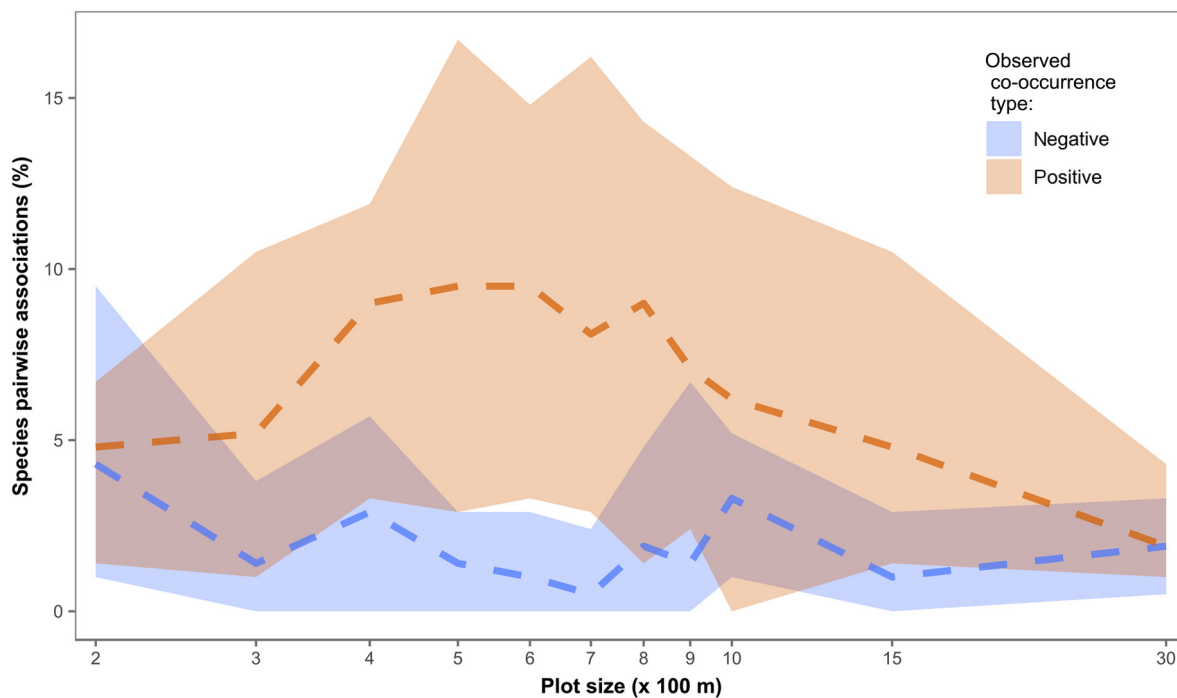
Fig. 2. Comparison of the percentage of significant positive (red) and negative (blue) co-occurrence types between pairwise species for different spatial scales. Dashed line is the percentage of significant pairwise species co-occurrences at $P = 0.05$ (significant level). Lower and upper borders of envelopes are the 0.01 and 0.10 significant levels, respectively.

of positive co-occurrences were due to determinants other than similarity in measured environmental conditions.

Effects of traits on co-occurrence

The relationships between species functional dissimilarity and the observed co-occurrence strength value were close to zero for the negative co-occurrences between pairwise species (central panel of Fig. 4; see also Appendix S1: Fig. S3 for forest composition). In other words, there was no relationship between the global species dissimilarity and the negative co-occurrence strength (top panels of the Fig. 4). For positive co-occurrences, the correlation coefficients with global species dissimilarities were significantly negative below 3000 m and highest for the 400-m plot scale (bottom panel of the Fig. 4). Thus, the more the species were functionally related, the more they showed positive co-occurrence. Similarities in animalivory,

herbivory, frugivory/granivory, and body mass showed significant negative correlation with species positive co-occurrences for ~400-m plot, whereas body mass also showed a similar pattern for the 3000-m plot scale (Fig. 5, Appendix S1: Figs. S4, S5).

Interacting species groups

Three distinct species groups were revealed by the cluster analysis (Fig. 6A). The first cluster was composed by four species, which have greater HR size (mean (log ha) = 6.15, overall mean = 4.14, V-test = 2.41). The second cluster gathered more than half of overall species (11 of 21), and regrouped species with a high frugivory/granivory (mean (%) = 80.8, overall mean = 66.95, V-test = 2.64) and a low animalivory (mean (%) = 8.61, overall mean = 20.7, V-test = −2.65) diet. There are six species in the third cluster, and no functional trait distinguished this cluster from the vertebrate assemblage.
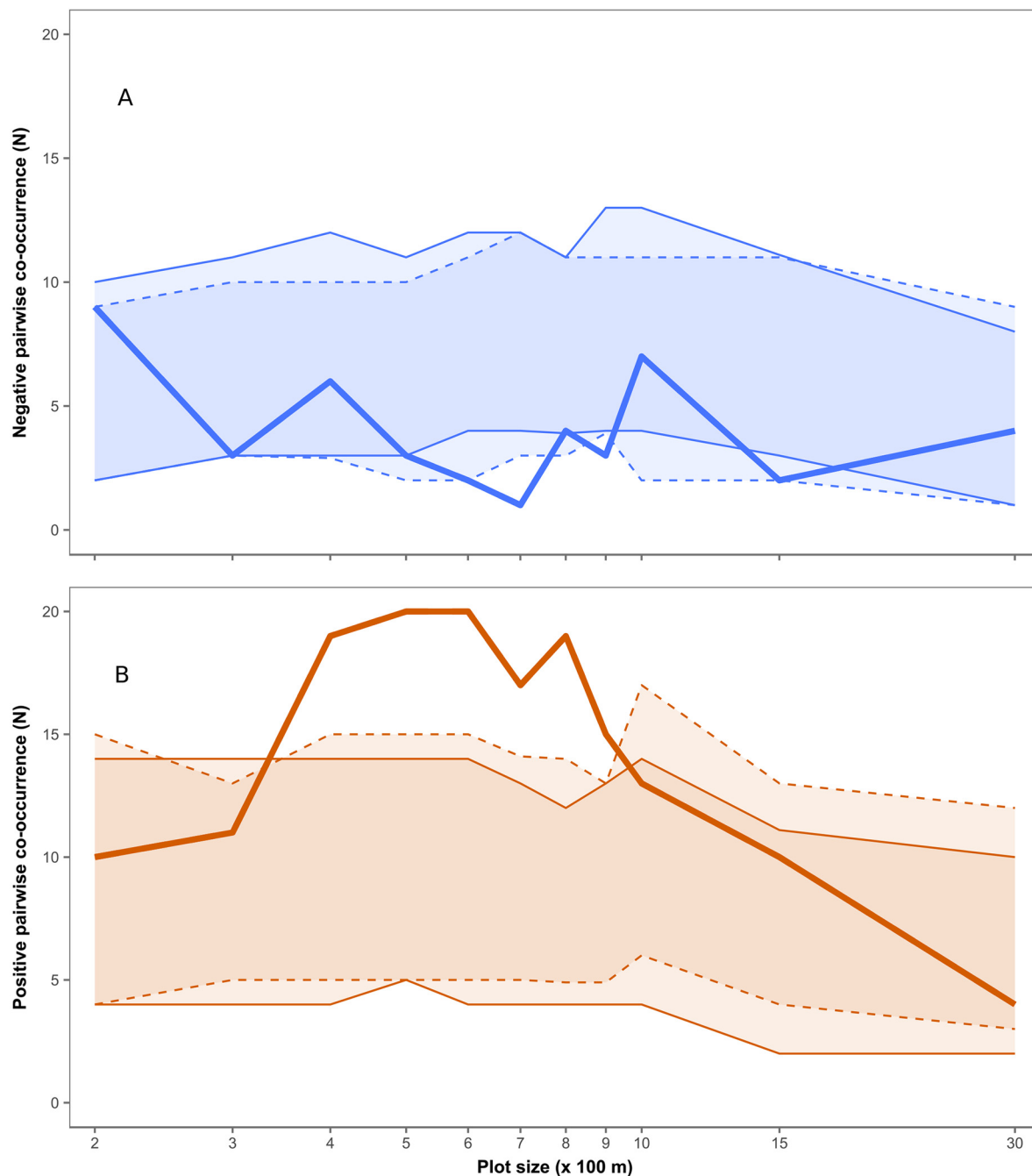
Fig. 3. Comparison of the observed number of negative (A) and positive (B) co-occurrences between pairwise species and the expected number (5th–95th quantile) under environmentally constrained models from forest structure (solid envelopes) or forest composition (dashed envelopes) environmental covariates.

DISCUSSION

Among our Neotropical vertebrate communities, negative co-occurrences were low enough to be considered as random (Fig. 2). Any actual competition process between pairs of vertebrates could have been counterbalanced by other ecological processes generating positive interspecific
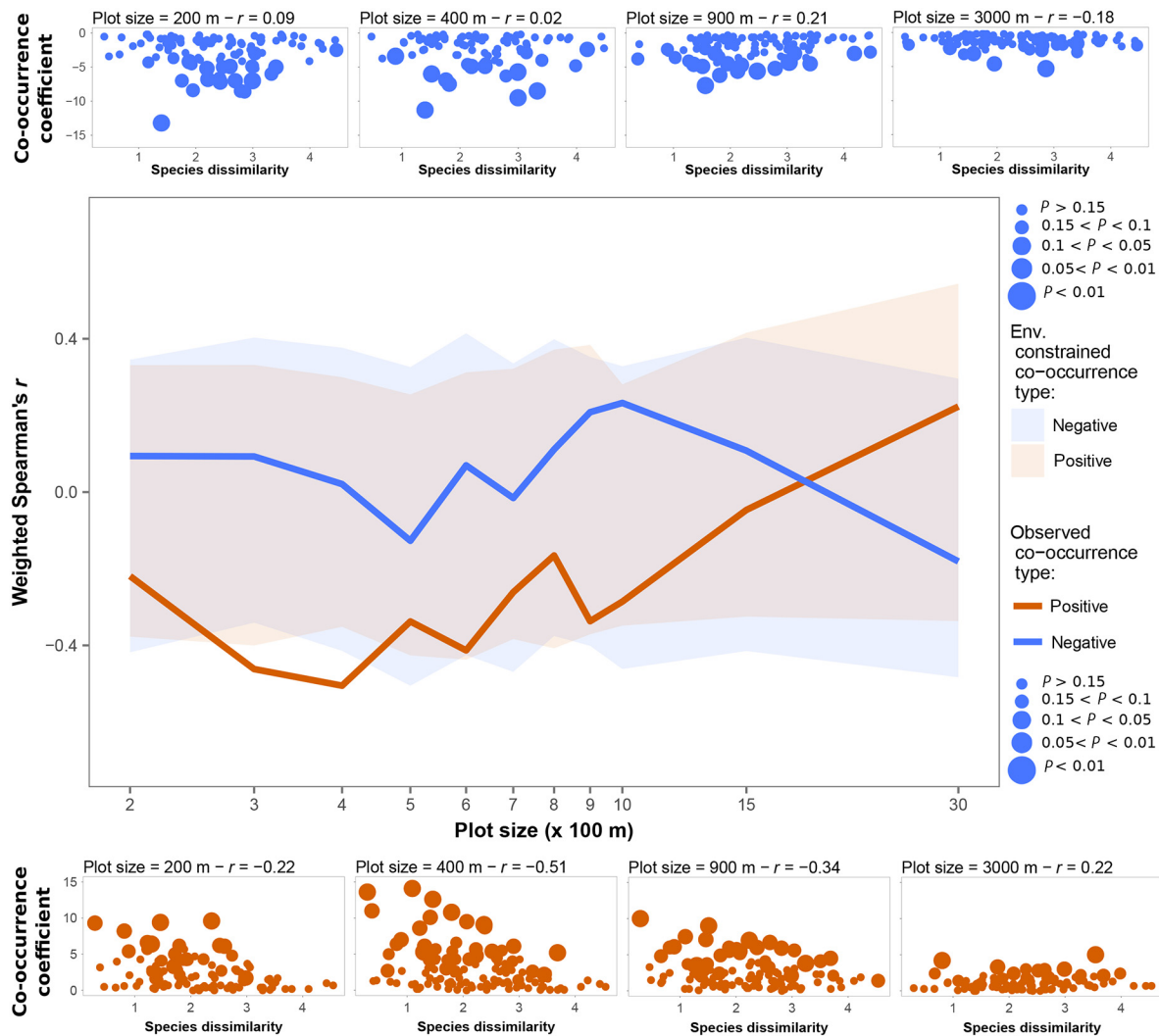
Fig. 4. Influence of species functional dissimilarity on the co-occurrence strength of unconstrained models and environmentally constrained models generated by forest structure. The weighted Spearman's r of each observed co-occurrence type is compared with those of the 5th–95th quantile ranges of distributions of the environmentally constrained models generated by forest structure (central panel). See similar results for forest composition (Appendix S1: Fig. S3). Top (negative co-occurrence) and bottom (positive co-occurrence) panels illustrate the observed relationship, from which the Spearman's r was calculated between the species dissimilarity and the co-occurrence strength for the 200-, 400-, 900-, and 3000-m plots. The co-occurrence strength was calculated as the difference between the observed and expected number of plots that the two species i and j co-occur (J_{ij}^{obs}-J_{ij}^{exp}; Veech 2014).

interactions (e.g., mutualism, commensalism, facilitation) or by environmental conditions and resource effects (e.g., requirements of similar habitat). On the other hand, the number of significant positive co-occurrence was high enough ($>5\%$) for us to conclude that these positive species co-occurrences were led by deterministic processes and were not generated by chance. At all scales of analysis, environment probably explains a part of these positive co-occurrences.
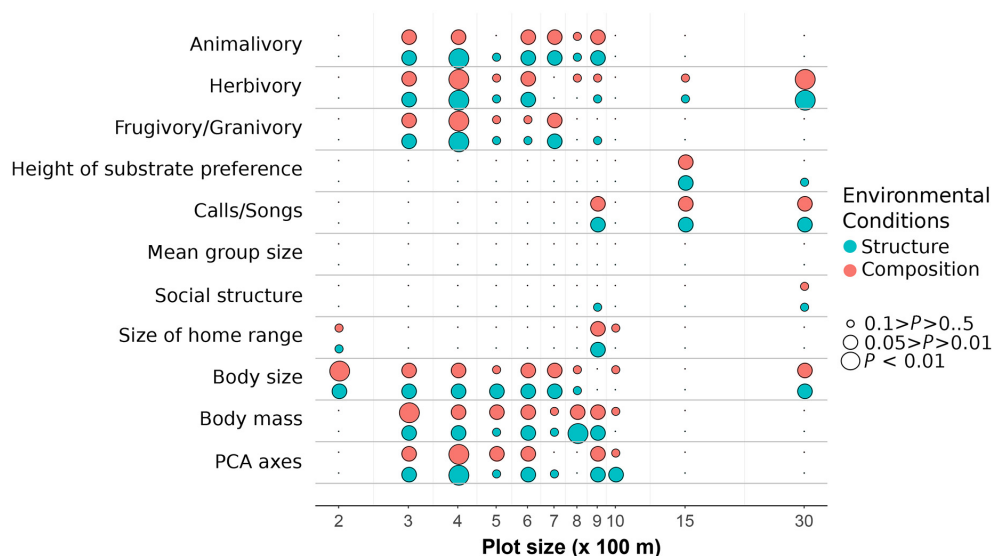
Fig. 5. Significance of univariate relationships between positive species co-occurrence strength and trait similarity. Levels of significance are shown for the environmentally constrained model at different spatial scales and are given for the forest structure and forest composition. Circle color corresponds to the component of the environmental conditions (forest structure and composition), and the circle size to the significance level of the relationship.

Effects of environmental conditions and spatial scale

Locally, environmental conditions may result in positive co-occurrence patterns (Kraft et al. 2015). Our results showed that environmental conditions partially explained observed positive co-occurrences (Fig. 3). At very small scale (200- to 300-m plots), forest structure and composition and/or topography is known to vary greatly in the Guiana Shield (Chave et al. 2003, Ferry and Morneau 2010, Guitet et al. 2018) and that could locally influence habitat use of medium- and large-sized vertebrates. Moreover, some spatially localized resources such as water, fruits, can be particularly important specially when they are in short supply. Finally, variation of forest productivity in relation to forest composition and to hydromorphologic soil conditions can temporally provide patchy resources to medium- and large-sized vertebrates (Ferry and Morneau 2010). Despite this, the number of co-occurrences attributable to the environment was low (Fig. 3). Altogether, this suggests that the effects of environmental conditions and negative interspecific interactions may confound each other, leading to

a low number of environment-induced co-occurrences at very small scale.

At large scale (up to 800-m plot in Fig. 3), habitat filtering and environment-driven assembly processes are generally considered to occur (Cavender-Bares et al. 2009). However, environmental conditions have already been shown to weakly shape medium- and large-sized vertebrate large-scale distribution in the Guiana Shield (Denis et al., 2016, 2017, 2018). All the studied species are indeed common across the sampled region, and their distribution only differs in relative abundance, thus not changing the presence-only co-occurrence pattern at these large scales.

Finally, positive co-occurrences dominate at intermediate spatial scale (from 400- to 800-m plots in Fig. 3), and our results showed that determinants other than pure environment may combine or add effects. A biological interpretation of midscale effects may be that a majority of our species have a HR ≤100 ha (14 species of 21 in Table 1) so that interspecific interactions should never reach a theoretical distance above ~1100 m, considering two strictly circular HRs.
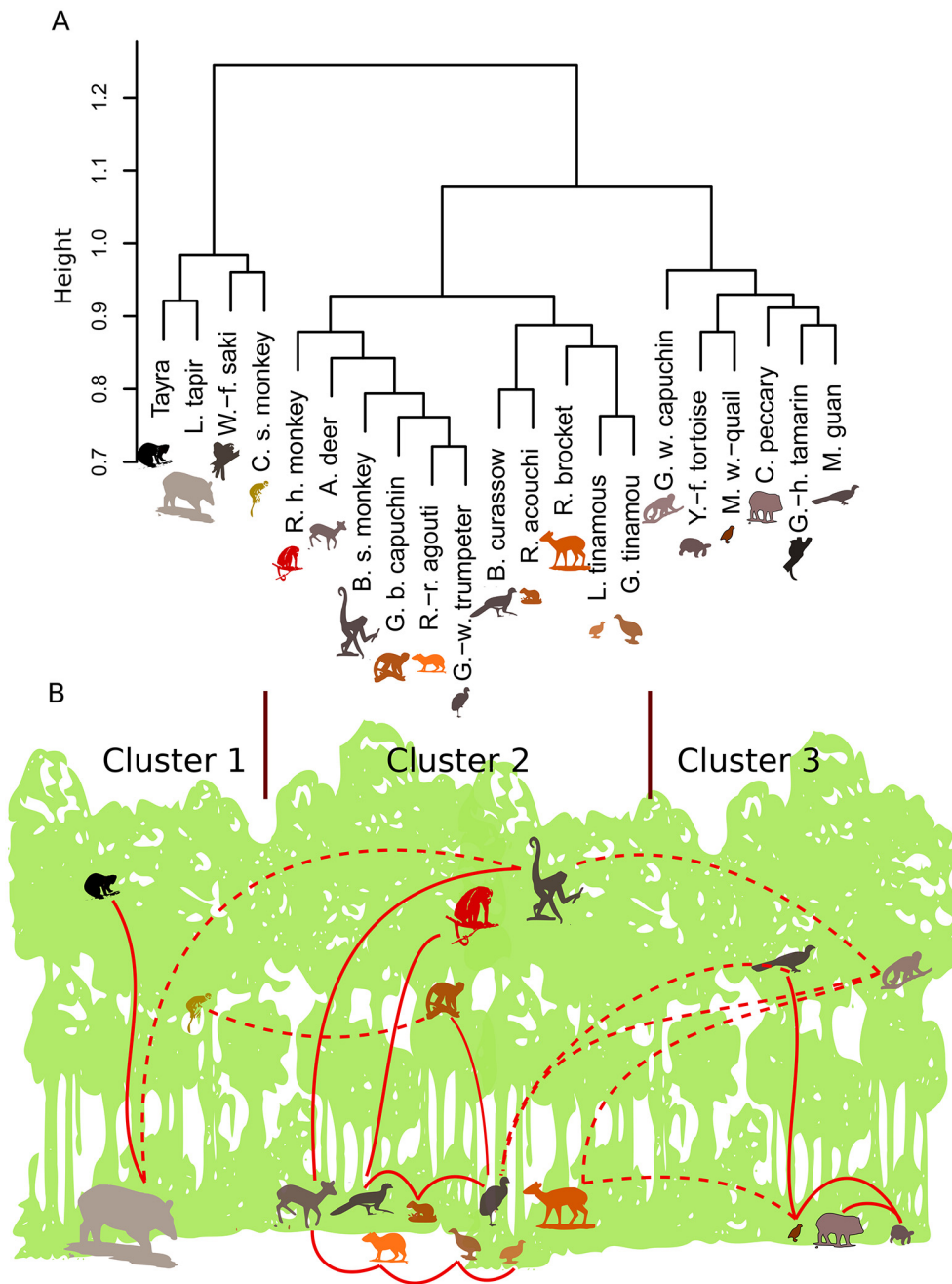
Fig. 6. (A) Cluster dendrogram of overall vertebrate assemblage based on Jaccard distance of species presence/absence. (B) Schematic illustration of presumed interspecific interactions (commensalism and mutualism). Positive co-occurrences between species pairwise are represented by red lines. We support that terrestrial species benefit by commensalism from feeding, foraging, and other behaviors of arboreal species. Solid and dashed lines represent positive co-occurrences within species groups and between species groups, respectively. Find after full common names sorted by initial letters and corresponding scientific names: Amazonian brown brocket deer, *Mazama nemorivaga* (F. Cuvier, 1817); Black curassow, *Crax alector* (Linnaeus, 1766); Black spider monkey, *Ateles paniscus* (Linnaeus, 1758); Collared peccary, *Pecari tajacu* (Linnaeus, 1758); Common squirrel monkey, *Saimiri*

(Fig. 6. *Continued*)

sciureus (Linnaeus, 1758); Guianan brown capuchin, *Sapajus [Cebus] apella* (Linnaeus, 1758); Golden-handed tamarin, *Saguinus midas* (Linnaeus, 1758); Great Tinamou, *Tinamus major* (Gmelin, 1789); Guianan weeper capuchin, *Cebus olivaceus* (Schomburgk, 1848); Grey-winged trumpeter, *Psophia crepitans* (Linnaeus, 1758); Lowland tapir, *Tapirus terrestris* (Linnaeus, 1758); Little tinamous, *Crypturellus* spp.; Marail guan, *Penelope marail* (Müller, 1776); Marbled wood-quail, *Odontophorus gujanensis* (Gmelin, 1789); Red acouchi, *Myoprocta acouchy* (Erxleben, 1777); Red brocket, *Mazama americana* (Erxleben, 1777); Red howler monkey, *Alouatta macconnelli* (Linnaeus, 1766); Red-rumped agouti, *Dasyprocta leporina* (Linnaeus, 1758); Tayra, *Eira barbara* (Linnaeus, 1758); White-faced saki, *Pithecia pithecia* (Linnaeus, 1766); Yellow-footed tortoise, *Geochelone denticulata* (Linnaeus, 1766).

This highlights the key role of spatial scale in shaping medium- and large-sized Neotropical vertebrate co-occurrence patterns.

On the key role of functional redundancy

We showed that positive co-occurrence strength is associated with functional similarity (Fig. 4). Positive co-occurrence patterns could be explained by the fact that functionally similar species do really benefit from each other with regard to food detection, food utilization, predator avoidance by matching activity (see examples for mixed-species bird flocks; Hutto 1988 and King and Rappole 2001). For example, enhance foraging success is an adaptive strategy when environmental severity is high and/or seasonally increases (Bruno et al. 2003).

In the Guiana Shield, medium- and large-sized vertebrates are seen sometimes together or close to each other, but they rarely form stable interspecific social groups (*personal observation*). Without the prominence of the so-called social groups in vertebrate assemblages, Seppänen et al. (2007) suggest that the (social) information exchange increases with the spatial proximity between different species (spatial co-occurrence) and their functional similarity (see Sridhar et al. 2012 and Norconk 1990, 's original works). Diet and body similarities are probably important at a relative fine spatial scale (Fig. 5), meaning that species would exchange information on, for example, the location of food and predation threat (see example in van Roosmalen 1985*b* for *Ateles paniscus*). For instance, heterospecific attraction are well known in waterbirds during migration. Individuals of a given species may use the presence of other species as an indicator of patch quality which conducted to positive co-occurrence patterns (Royan et al. 2016). The potential value of such information for survival and the associated negative interactions (e.g., an increase in competition for resources) may form a typical trade-off situation (Seppänen et al. 2007).

On the importance of diet and body size in medium- and large-sized vertebrates

Because of their similarities in body size and diet (Appendix S1: Figs. S4, S5), frugivores of similar size tend to co-occur in space, probably to consume similar fruits (Peres et al. 2016). So, our local vertebrate assemblages are characterized by species groups with high functional redundancy that (1) exhibit similar ecological functions and that (2) exploit the same type of available resources. This contrasts with the common prediction that smaller sized vertebrates gain advantages by joining larger ones to defend against predators and/or by resource partitioning (Arsenault and Owen-Smith 2002, Stensland et al. 2003, Sridhar et al. 2012). However, species similarities based on sociability traits or preference of substrate height had no effects on positive co-occurrence strength (Fig. 5), and thus possibly did not intervene in positive interspecific interactions.

In the rainforest three-dimensional space, terrestrial frugivores depend mainly on tree fruits that are directly available to them in the understory (e.g., for larger birds), and/or that fall from canopy and reach the ground (e.g., for ungulates or larger rodents). Field observations have showed that, through different behavior mechanisms, terrestrial vertebrates benefit from feeding and foraging of arboreal vertebrates (*personal observation*; Torres 1997, Newton 1989, Santamaria and Franco 2000, van Roosmalen 1985*b* and Erard et al. 2007 for one counterexample). For example, in India, Chital deer (*Axis axis*) benefit from vegetation dropped by langur monkeys (*Presbytis entellus*). In the Guiana Shield, several terrestrial mammals (agoutis, acouchis, deer, and

peccaries) and birds (black curassow and grey-winged trumpeter) come to eat fruits dropped by primates. Thus, observed positive co-occurrences between more frugivore/granivore species support field observations and show that arboreal vertebrates could have an unidirectional positive (commensalistic) interactions on the terrestrial vertebrates by ameliorating the food resource availability and promote species co-existence (red lines between arboreal and terrestrial vertebrates in Fig. 6B).

In oligotrophic *terra firme* forests of Amazonia and during dry season (when data were collected), resources are scarce (Stevenson et al. 2000, Haugaasen and Peres 2005). Medium- and large-sized vertebrates are forced to focus on scarce and dispersed resources. In these circumstances, the patchy resource distribution in space (e.g., fruits or flowers) had probably affected the observed co-occurrences, leading to positive patterns. Resource distribution in space can be relatively independent of environmental conditions when, for example, flowering or fruiting phenology are not well synchronized within tree species (Kraft et al. 2015).

Conclusion

Scrutinizing the spatial scales to study species co-occurrence patterns reveals the existence of structuring force in medium- and large-sized vertebrate assemblages, and clearly highlights the importance of spatially explicit analysis. At a fine scale, environmental conditions partially explained the highlighted positive co-occurrence patterns. Moreover, since functionally similar species tend to occur together, functional redundancy within species groups plays probably a key role in species co-existence. Finally, our work indicates that diet and body size are likely of primary importance in species interactions between terrestrial and arboreal vertebrates in Neotropical rainforests and that resource distribution is not only related to environmental conditions. Our findings pave the way to a better understanding of the role of more deterministic processes shaping Neotropical faunal communities. Future research should focus on species population growth rates in light of functional traits to understand how interspecific interactions affect species demography.

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