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Site and species contribution to β-diversity in terrestrial mammal communities: evidence from multiple Neotropical forest sites

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ABSTRACT

In a scenario where escalating human activities lead to several environmental changes and, consequently, affect mammal abundance and distribution, β-diversity may increase due to differences among sites. Using the ecological uniqueness approach, we analyzed β-diversity patterns of ground-dwelling mammal communities recorded through comprehensive camera trap monitoring within eight tropical forests protected areas in Mesoamerica and South America under variable landscape contexts. We aimed to investigate whether the contribution of single sites (LCBD) and single species (SCBD) to overall β-diversity could be explained by community metrics and environmental variables, and by species metrics and biological traits, respectively. Total β-diversity was also partitioned into species replacement and richness difference. We related LCBD to species richness, total relative abundance, functional indices, and environmental variables (tree basal area, protected area size, NDVI, and precipitation seasonality), and SCBD to species naïve occupancy, relative abundance, and morphoecological traits via beta regression. Our findings showed that LCBD was primarily explained by variation in species richness, rather than relative abundance and functional metrics. Protected area size and tree basal area were also important in explaining variation in LCBD. SCBD was strongly related to naïve occupancy and relative abundance, but not to biological traits, such as body mass, trophic energy level, activity cycle, and taxonomic category. Local β-diversity was a result of species replacements and to a lesser extent differences in species richness. Our approach was useful in examining and comparing the ecological uniqueness among different sites, revealing the regional scale current status of mammal diversity. High LCBD values comprised sites embedded within smaller habitat extents, hosting lower tree basal areas, and harboring low species richness. SCBD showed that relatively ubiquitous species that occur at variable abundances across sites contributed most to β-diversity.

KEYWORDS: camera trapping monitoring, conservation, ecological uniqueness, LCBD, large-bodied mammals, protected areas.

1. Introduction

Community structure and diversity result from complex and dynamic phenomena, determined by a large number of processes in space and time (Ricklefs, 2006). Understanding patterns of species distribution at different scales (i.e., local, regional, and global) and the factors that govern these patterns have been central goals in ecology research (Chase, 2003; Gaston, 2000; Jetz and Fine, 2012; Ricklefs, 1987). The concept of species diversity encompasses multiple spatial scales, comprising what we know as α-diversity, corresponding to the number of species at individual sites, γ-diversity, related to the diversity of entire geographic regions, and β-diversity or the variation in species composition among sites within a region (Whittaker, 1972).

Since its conceptualization, β-diversity has become a key to a better understanding of the origin, functioning, and maintenance of biodiversity (Legendre, 2014; Legendre et al., 2005). Different indices and methods have been proposed to estimate β-diversity, using presence-absence or abundance data, multiplicative indices, additive partitioning of community diversity (Baselga, 2010; Koleff et al., 2003; Legendre et al., 2005; Lennon et al., 2001), and also by incorporating phylogenetic and functional relationships among species (Ricotta and Burrascano, 2008; Stegen and Hurlbert, 2011; Swenson, 2011). In a global scenario where escalating human activities lead to disturbance, habitat loss, fragmentation, and climate change affects species abundance and distribution, variation in community composition may increase due to differences in local extinction, competition, and colonization rates among sites (Legendre, 2014; Socolar et al., 2016; Thornton et al., 2011; Urban, 2015). To deal with biodiversity loss and draw up effective conservation plans we need a better understanding of the mechanisms that maintain local and regional diversity (Legendre, 2014; Legendre et al., 2005). Measured appropriately, changes in β-diversity provide the scaling factor that allows us to predict changes in γ-diversity from measured changes in α-diversity (Socolar et al., 2016). In this context, β-diversity indices have become an important tool to understand the effects of landscape modification on species assemblages. These studies have spanned different taxa, including plants (Bergamin et al., 2017; Grass et al., 2015; Heydari et al., 2017), insects (Kim et al., 2018; Van Allen et al., 2017), birds (Grass et al., 2015; Meynard et al., 2011), and mammals (Palmeirim et al., 2018; Pardini et al., 2005).

In a recent advance, Legendre and De Cáceres (2013) developed a method that uses a species-by-site abundance matrix to estimate the total variance found in a community (i.e., the Total β-diversity - BD_{Total}), which can be further decomposed into contributions of the individual sites and the individual species to overall β-diversity. Local contributions to β-diversity (hereafter, LCBD) indicate the degree of ecological uniqueness of each sampling site. From a conservation planning perspective, large LCBD values indicate sites that have either unusual species combinations of high conservation value or degraded and species-poor sites that may be prioritized for ecological restoration (Legendre, 2014). Thus, sites presenting high LCBD values are not obligatorily the sites exhibiting hyper-diversity or harboring rare species, but those sites more different from most of the other sites (Borcard et al., 2018; Heino and Grönroos, 2017). Various studies have been associated LCBD values with community metrics, environmental conditions, and anthropic activities, aiming to explain these patterns and recognize which characteristics can predict ecological uniqueness (da Silva et al., 2020; Heino and Grönroos, 2017; Li et al., 2020; Vilmi et al., 2017). For example, findings on insect stream communities have shown that most of the impacted streams exhibiting high LCBD values and lower α-diversity may be associated with sites harboring species that are more tolerant of anthropic impacts (de Paiva et al., 2021). On the other hand, species contribution to β-diversity (hereafter, SCBD) represents the degree of the relative importance of individual species to β-diversity across sites and can be used to identify which species contribute the most to dissimilarity among communities or require specific attention (Legendre and De Cáceres, 2013). As observed from empirical studies, SCBD values tend to increase when species presented a large variation in abundance and were well distributed across sites (Heino and Grönroos, 2017; Legendre and De Cáceres, 2013). Also, SCBD may be associated with species characteristics, such as niche position and niche breadth, or species biological traits (body size, diet, dispersal capacity, and others). These ecological and biological characteristics may be intercorrelated, reflecting species-environment associations, and are useful to reveal which kind of species are particularly important to understand the formation of β-diversity (da Silva et al., 2018, Heino and Grönroos, 2017).

The study of β-diversity also benefited from applicable approaches that compute the partitioning of the total variation of community composition into two components, species replacement (or turnover) and richness difference (and nestedness) (Legendre and De Cáceres, 2013; Lennon et al., 2001). The partitioning aims to evaluate the influence of various processes on the patterns of β-diversity (Baselga, 2010; Legendre, 2014; Leprieur et al., 2012). Thus, species replacement occurs when species are replaced by others along an ecological gradient, according to their ecological optima or niche breadth. This pattern may be explained by environmental forcing, competition, and/or historical events (i.e., disturbances), i.e., it reflects the influence on the community structure of the variables controlling ecological gradients (Legendre, 2014). Meanwhile, richness difference may be caused by local species disappearances, local abiotic conditions and numbers of available ecological niches, or other ecological processes leading to communities with higher or lower numbers of species (Legendre, 2014; Legendre and De Cáceres, 2013).

Considering ecological uniqueness, this study is focused on terrestrial Neotropical mammals, a key functional group, as they fulfill multiple trophic roles including apex predation, herbivory, seed predation, and seed dispersal (Lacher et al., 2019; Terborgh et al., 1999). Also, medium and large-bodied Neotropical mammals often have considerable dispersal capacity and can occupy the most diverse types of landscape physiognomy (Eisenberg, 1990; Jones and Safi, 2011), making them a unique group to understand patterns of diversity and responses to disturbances. β-diversity of mammal communities is affected by differences in habitat quality and heterogeneity (Kerr and Packer, 1997; Melo et al., 2009), and is also related to species richness and ecological functions (da Silva et al., 2020). To our knowledge, only one study has examined how variation in mammal ecological uniqueness can be explained by taxonomic and functional features at large spatial extents (da Silva et al., 2020), and no study has investigated the relationships between SCBD and mammal species metrics and biological traits.

In this context, we aimed to fill this gap by focusing on Neotropical terrestrial mammal communities across eight protected forests in Mesoamerica and South America, which are under different landscape contexts (i.e. fragmented or intact forests), and contain different species compositions and abundances (Ahumada et al., 2011; Santos et al., 2019). Specifically, we were interested in assessing whether LCBD indicates taxonomic and functional changes in mammal communities and the environmental drivers underpinning these changes at regional scales, and how individual species (SCBD) contribute to the overall β-diversity. Thus, we hypothesized that community metrics and environmental conditions would influence LCBD. We expected that generalist mammal species, exhibiting broad niche spaces, would contribute less to β-diversity than species with small to intermediate-sized niches, as other taxonomic groups (da Silva et al., 2018; Heino and Grönroos, 2017; Vilmi et al., 2017). Finally, as total β-diversity (BD_{Total}) can be partitioned into species replacement and richness difference, we expected that the ecological uniqueness of most of our sites would result from the species replacement process, i.e., β-diversity is a result of simultaneous species gains or losses due to environmental filtering, competition, or historical events, rather than just the variation in the number of co-occurring mammals species (Borcard et al., 2018; Legendre, 2014).

2. Material and Methods

2.1. Study sites

We used data from eight Neotropical forest sites that are part of the Tropical Ecology Assessment and Monitoring (TEAM) Network, a global standardized biodiversity monitoring program (Beaudrot et al., 2016; Rovero et al., 2020). Neotropical TEAM sites are distributed across six countries in Central and South America: Volcán Barva Transect, Costa Rica (VB), Barro Colorado Nature Monument, Panamá (BCI), Central Suriname Nature Reserve, Suriname (CSN), Yasuní National Park, Ecuador (YAS), Caxiuanã National Forest, Brazil (CAX), Manaus, Brazil (MAN), Cocha Cashu - Manu National Park, Peru (COU) and Yanachaga National Park, Peru (YAN) (Fig. 1).

Following the categorization criteria for landscapes adopted by Beaudrot et al. (2016), study sites were divided into intact and fragmented protected forest landscapes. Intact forest landscapes are those in which protected areas were either indistinguishable from the continuous forest in surrounding areas (i.e., CAX, COU, CSN, and YAS), and fragmented forest landscapes are those in which protected areas were embedded within a patchwork mosaic of forest and non-forest areas (i.e., BCI, MAN, VB, and YAN).

2.2. Mammal surveys

Medium to large-bodied ground-dwelling terrestrial mammals (henceforth, terrestrial mammals) were sampled during a camera trapping monitoring program conducted between 2010 and 2014. The sampling design at each site consisted of a regular grid of 60 camera trap stations (or two grids of 30 camera trap stations each) spaced apart by ≈1.4 km. The sampling period at each study site occurred within the dry season months and cameras remained in the field for at least 30 days, once a year (Jansen et al., 2014; TEAM Network, 2011). Our dataset comprised four sampling periods at each study site (excepted for Manaus, where data were available only for 2010 and 2011). Camera traps (Models RM45 and HC500, Reconyx Inc.) were configured to take three pictures per trigger with no delay or intervals between photos, working 24 hours/day. No baits were used to attract animals, and cameras were deployed off trails. Our sampling design exceeds the recommendations, in terms of sampling effort and camera trap stations, to obtain reliable estimates of species richness, occupancy, and relative abundance using standardized monitoring of terrestrial mammal species on a large spatial scale (Kays et al., 2020).

Images of the same species were considered independent detections when at least one hour had passed between consecutive photographs (Rovero and Spitale, 2016). For data analysis, we excluded images of species that were primarily arboreal (e.g., primates) and water-dependent, to avoid sampling bias or particularities of any given study area. We also pooled some congeneric species into an "ecospecies" taxon, thereby avoiding overestimating mammal assemblage differences between study sites that contained ecologically analogous species (for example, *Nasua narica* and *Nasua nasua* represent unique ecospecies '*Nasua*') (Emmons and Feer, 1997; Jones et al., 2009). To streamline, we hereafter use "species" to refer to both species and ecospecies.

2.3. Explanatory variables

2.3.1. Biological traits

We gathered information for five biological traits: body mass, trophic energy level, activity cycle, and taxonomic category (Order). These traits describe physiological, behavioral, and ecological characteristics that determine species' role and function in ecosystems (Wilman et al., 2014). Body mass, trophic energy level, and activity cycle (activity time categories) were set based on species-level datasets that describe species biological key attributes (Jones et al., 2009; Wilman et al., 2014).

The species body mass corresponds to the adult weight in grams. For trophic energy levels, we weighted the proportion of each major dietary mode of any given species by the energetic levels, grouped as modal dietary patterns, as follows: (1) folivore < (2) frugivore/nectarivore < (3) granivore < (4) insectivore/myrmecophage < (5) carnivore (Benchimol and Peres, 2015; da Silva et al., 2020; Wilman et al., 2014). For example, if a raccoon (*Procyon* spp.) consumes 50% invertebrates, 30% vertebrates, 10% fruits, and 10% seeds, its trophic level would be 4 [i.e., (0.5 × 4) + (0.3 × 5) + (0.1 × 2) + (0.1 x 3)]. The activity cycle represents an ordinal assignment of the period of activity for each species. Species were defined as (1) nocturnal only, (2) nocturnal/crepuscular, cathemeral, crepuscular or diurnal/crepuscular, and (3) diurnal only (Jones et al., 2009). We used Order as a category grouping phylogenetically related species (Emmons and Feer, 1997; Paglia et al., 2012).

2.3.2. Community and species metrics

Community metrics included four variables: species richness, relative abundance, and two functional indices, functional richness and functional divergence. Species richness was expressed as the total number of species recorded at each sampling period and site, while relative abundance index (RAI) was estimated as the ratio between the total number of images for all species at each site and the total sampling effort at each site expressed as the total number of images/total camera traps-days (Carbone et al., 2001; O'Brien, 2011). Relative abundance provides information on population abundance, especially when it's difficult to estimate true species abundance, and it is positively related with independent density and abundance estimates (Carbone et al., 2001; O'Brien, 2011; Palmer et al., 2018).

Functional indices were calculated using species *versus* species traits (as described in 2.3.2 section) matrices. We applied Gower's general distance coefficient, which integrates several types of variables (e.g., quantitative, nominal, fuzzy, ordinal, circular, etc.) to compute the functional distance between each pair of species, using functions from the R package 'ade4' (Dray and Dufour, 2007; Pavoine et al., 2009). Therefore, we used the functional distance matrix among all species to calculate both functional diversity indices using the dbFD function of the 'FD' package in R (Laliberté et al., 2014). Functional richness (F_{Ric}) represents the amount of functional space filled by the community, with low values indicating that some of the resources potentially available to the community are unused (Mason et al., 2005). Functional divergence (F_{Div}), weighted by species abundances, relates to how abundance is distributed within the volume of functional trait space occupied by species (Villéger et al., 2008). High functional divergence indicates a high degree of niche differentiation, and presumably low resource competition (Mason et al., 2005). There are various functional diversity indices and many of them can be highly correlated (Mouchet et al., 2010), but our choice was based on findings that both of these functional indices are related to ecological uniqueness (da Silva et al., 2020).

Species metrics included two variables: naïve occupancy and relative abundance. Naïve (or observed) occupancy was measured as the proportion of camera trap points where the species was recorded. It reflects the extension of the species' presence across the sampling area, ranging from 0 (a species does not occur in any camera trap station) to 1 (a species occurs in all camera trap stations) (Rovero and Spitale, 2016). The relative abundance index, as described above, was estimated by the total number of records of each species per sampling effort at each site, expressed as the number of images/camera traps-days (Carbone et al., 2001; O'Brien, 2011).

2.3.3. Environmental variables

Environmental covariates were selected based on forest structure and bioclimatic conditions that have been shown to influence the distribution and diversity of mammals (Maestri and Patterson, 2016; Qian, 2009). For each study site, we recorded (1) elevation, (2) NDVI (Normalized Difference of Vegetation Index), (3) tree density (tree/ha), (4) tree basal area, (5) mean annual temperature, (6) mean annual precipitation, (7) precipitation seasonality (coefficient of variation), and (8) protected area size.

Elevation data were extracted from a digital elevation model (DEM) based on the NASA Shuttle Radar Topographic Mission (SRTM), with a spatial resolution of one arc-sec (≈ 30m). DEM data were downloaded from the U.S. Geological Survey (Earth Explorer, 2017) and pooled estimates were obtained using QGIS software (QGIS

Development, 2015). NDVI was generated from Landsat TM and ETM+ satellite imagery across the core study areas. The acquisition date of each image matched the first year of camera trap deployment at each site [data from (Rovero et al., 2020)].

Mean values for tree density and tree basal area were calculated from six 1-ha plots inventories within each of the eight sites [Data available from the TEAM Network database; See information on (TEAM Network, 2010)]. Tree density measurements consist of the number of trees larger than 10cm in DBH within each one-hectare plot. The total basal area, measured as m^2/ha, was calculated across the six 1-ha plots. Bioclimatic data were sourced from WorldClim - Global Climate Database based on a 30-sec spatial resolution (~1 km^2) (Fick and Hijmans, 2017). Climate variables (temperature, precipitation, and seasonality) were extracted through a script using the R software (Team R Core, 2018). To estimate the protected area size we extracted the polygon of the protected area for each study site from the World Database on Protected Areas (WDPA) and calculated the area of each protected site in hectares after reprojecting the polygons to the appropriate local (UTM) coordinate system [data from (Beaudrot et al., 2016; Rovero et al., 2020)].

2.4. Data Analysis

2.4.1. BD_{Total}, LCBD, and SCBD

We calculated the local contribution to β-diversity (LCBD) and species contribution to β-diversity (SCBD) following the approach proposed by Legendre and De Cáceres (2013), which uses the total variance of the community data Table Y (the abundance values of *p* species observed in *n* sampling units) as an estimate to the total β-diversity (BD_{Total}). The variance, Var(Y), consists of computing a matrix of squared deviations from the column means. Firstly, we Hellinger-transformed the abundance-based species-by-site community matrix and, subsequently, we calculated the squared difference between each Hellinger-transformed value and the mean abundance of the corresponding species. The elements of this matrix containing the squared differences are summed up to obtain the total sum of squares (SS_{Total}). Then, BD_{Total} is obtained by dividing the total sum of squares by the number of sites minus 1.0 [BD_{Total} = Var(Y) = SS_{Total} / (n -1)] (Legendre and De Cáceres, 2013). BD_{Total} is in the range [0, 1], so the maximum value is reached if all sites have entirely different species compositions when compared to one another.

From the BD_{Total} computed, we assessed the contribution of individual sites (LCBD) and individual species (SCBD). LCBD of a given site is calculated by dividing the sum of squares corresponding to this site by the total sum of squares. LCDB values are comparative indicators of the ecological uniqueness of the sites in terms of community composition, computed as the relative contribution of a site to BD_{Total} so that the LCBD indices sum to one (1.0). SCBD coefficients represent the degree of variation of individual species across all sites, indicating how much a species contributes to overall β-diversity. The contribution of a species '*j*' is the sum of the centered and squared values for species '*j*' in the matrix, divided by the total sum of squares. The species with above-average SCBD values were the most important contributors to BD_{Total} (Borcard et al., 2018; Legendre and De Cáceres, 2013).

LCBD and SCBD indices were computed using the beta.div function available from the 'adespatial' package in R (Dray et al., 2018). We assessed differences in LCBD indices among all eight-study sites using ANOVAs and associated multiple Tukey's HSD comparisons for pairwise differences among sites, after checking for assumptions of homogeneity and normality of variance (Levene's Test for Homogeneity of Variance and Shapiro-Wilk normality test, respectively). All statistical tests were considered significant at a p-value < 0.05.

To assess which of the two processes, species replacement or richness/abundance difference, best explain variation among mammal communities, we used the beta.div.comp function of the 'adespatial' R package to partition the total β-diversity (Borcard et al., 2018). This method is used for both presence-absence and abundance data, computing the dissimilarity, replacement, and richness or abundance difference. Local replacement (*Repl*) and richness/abundance differences (*RichDiff/AbDiff*) measure how unique each site is compared to the other, in terms of either replacements or richness/abundance differences (Legendre and De Cáceres, 2013). As we have species-by-site abundance data, we used the Ružička dissimilarity index, which is the quantitative equivalent to the Jaccard index (Legendre, 2014). Therefore, we used Podani's Jaccard-based indices to extract the dissimilarity (*D*), replacement (*Repl*), and richness/abundance difference (*RichDiff/AbDiff*) matrices. The function output produces a list containing these three matrices, as well as global results: BD_{Total}, total replacement diversity ($Repl_{Total}$), and total richness/abundance diversity ($RichDiff_{Total}/AbDiff_{Total}$) (Borcard et al., 2018).

2.4.2. Statistical modeling

We used beta regression analysis to examine patterns of site contributions (LCBD) and species contributions to β-diversity (SCBD). We choose beta regression as our modeling tool because it is more appropriate when response data range between 0 and 1 (Cribari-Neto and Zeileis, 2010), as our LCBD and SCBD indices. Beta regression is based on the assumption that the dependent variable is beta-distributed and that it is related to a set of regressors through a linear predictor with unknown coefficients and a link function (Cribari-Neto and Zeileis, 2010).

We used beta regression with a logit link function for models including LCBD and SCBD as the response variable. First, we related LCBD to community metrics: species richness, community relative abundance, functional richness (F_{Ric}), and functional divergence (F_{Div}). Second, we attempted to explain LCBD using environmental variables as predictors. Before analyses with environmental variables, we calculated the variance inflation factor (VIF) to detect multicollinearity between predictors in our models. Only variables with VIF < 3 were incorporated into the model. From the eight environmental variables measured, only NDVI, tree basal area, precipitation seasonality, and protected area size were retained.

In the next step, we related SCBD to species metrics: species naïve occupancy and species relative abundance. Because these metrics were correlated (Pearson Correlation = 0.836), we modeled SCBD values independently for each species metrics. Finally, we examined variation in SCBD using species traits: body mass, trophic energy level, activity cycle, and order. When relating SCBD values with these metrics, we aimed to verify if species that contribute most to β-diversity are those with a small or intermediate-sized ecological niche.

We ran beta regression analyses using the betareg function from the ‘betareg’ R package (Cribari-Neto and Zeileis, 2010). We also examined reduced models based on pseudo coefficients of determination (pseudo-R^2). We calculated VIF and the correlation coefficients using the ‘car’ and ‘stats’ R packages (Fox and Weisberg, 2018).

3. Results

A total of 30,870 terrestrial mammal images were recorded across all eight study sites, representing an overall γ-diversity of 48 taxonomic species (= 33 ecospecies) representing 30 genera. The number of species per site (α-diversity) ranged from 16 to 27 species (23.12 ± 3.75 species; mean ± SD) (Fig. 2a; see Appendix A.1 in Supporting Information for a complete species checklist per site). Most species were shared among two or more study sites, and just two species were exclusive to a single site: *Canis latrans* (Coyote) at BCI and *Tremarctos ornatus* (Spectacled bear) at YAN, but they were rarely recorded (2 and 1 images, respectively). Total relative abundance was significantly different among sites ($F = 103.1$, $df = 7$, $p = 0.001$), with BCI and VB containing the highest and lowest values, respectively (Fig. 2b; Appendix A.2). The most abundant species was *Dasyprocta* spp. (Agouti), a medium-sized diurnal rodent recorded at all sites. Other species were often abundant whenever present, such as *Cuniculus paca* (Spotted paca), *Mazama* spp. (Red brocket deer), *Pecari tajacu* (Collared peccary), and *Dasypus* spp. (armadillos, corresponding to *D. novemcinctus* and *D. kappleri*; Fig. 2a; Appendix A.3 in Supporting Information).

3.1. β-diversity: LCBD and SCBD metrics

The total β-diversity (BD_{Total}) was 0.195 across all mammal communities. The local contribution of individual sites (LCBD) ranged from 0.023 to 0.050, indicating the uniqueness of the mammal community at each study site. Sites with the highest uniqueness in species composition were VB, YAN, MAN, and BCI. Comparisons between sites evidenced significant compositional differences ($F = 14.61$, $df = 7$, $p = 0.001$; Fig. 3a), highlighting significant differences in pairwise comparisons between the four sites mentioned above and all other sites (COU, CSN, CAX, and YAS; Appendix A.4 in Supporting Information).

Regarding SCBD, values ranged from 0.0001 to 0.2612 and nine species contributed to β-diversity well above the mean (> 0.0303) of the 33 species: *Myoprocta* spp. (acouchy), *Pecari tajacu* (collared peccary), *Dasyprocta* spp. (agouti), *Cuniculus paca* (paca), *Mazama nemorivaga* (Amazonian brown-brocket deer), *Tapirus* spp. (tapir), *Mazama* spp. (Red brocket deer including the allopatric *M. americana* and *M. temama*), *Didelphis marsupialis* (common opossum), *Sciurus* spp. (midsized squirrels) (Fig. 3b, Appendix A.5 in Supporting Information).

Partitioning BD_{Total} revealed a slightly higher percentage of total richness difference ($RichDiff_{Total}$ = 0.140; 57%) than its replacement component ($Repl_{Total}$ = 0.107; 43%), showing that difference among mammal communities resulted from both processes. Considering study sites individually, species dissimilarities at BCI and YAS largely resulted from the richness difference component (>95%), while differences among the other six sites resulted from large proportions of species replacement (>60%, Fig. 4).

3.2. Explaining LCBD and SCBD

Our model for the two community metrics examined here indicated that LCBD was negatively related to species richness (β = -0.093, z = -3.336, p = 0.001) but exhibited no significant association with total relative abundance, functional richness (F_{Ric}), and functional divergence (F_{Div}) (Table 1, Fig. 5a). The model including environmental covariables showed that tree basal area (β = -0.209, z = -4.327, p = 0.001) and protected area size (β = -0.339, z = - 8.308, p = 0.001) were negatively associated with LCBD (Table 1, Fig. 5b and 5c).

Beta regressions for the species metrics showed a positive effect for naïve occupancy (β = 4.666, z = 8.59, p = 0.001), while relative abundance also presented a positive effect but with lower ratio values ($\beta = 0.430$, $z = 3.951$, $p = 0.001$; Fig. 6). Beta regression also showed that none of the biological traits tested were significant predictors to SCBD (Table 2).

4. Discussion

Our findings showed that both the local (LCBD) and species contributions (SCBD) to β-diversity are important in understanding the current conservation status of mammals across our eight Neotropical forest sites. Our data support our predictions that community metrics and environmental characteristics would influence ecological uniqueness. However, our expectations that ecological uniqueness could also be affected by relative abundance and functional diversity were not confirmed. SCBD was strongly related to species metrics but not with species traits, showing that highly ubiquitous and highly abundant species contributed most to β-diversity. We next discuss these main findings in further detail.

We found a low value of BD_{Total} (0.195 from a maximum of 1), which suggests that our study sites were similar in their mammal species composition and hosted relatively few exclusive species. This is a predictable pattern because all our study sites are located within the same major tropical moist broadleaf forest biome, and therefore share similar habitat characteristics, species interactions, and history (Olson et al., 2001). In general, ground-dwelling medium to large-sized mammals have a wide geographic distribution [e.g., *C. paca* or *P. onca* (jaguar)] or are replaced by allopatric or parapatric congeners throughout the region (Eisenberg, 1990; Emmons and Feer, 1997). For example, several closely related congeners [e.g., *Mazama americana* and *M. temama* (red-brocket deer), *Nasua narica* and *N. nasua* (coatis), and *Dasyprocta leporina*, *D. punctata*, and *D. fuliginosa* (agoutis)] were recorded at different sites.

Among most of our mammal communities, dissimilarity was a result of species replacement and to a lesser extent richness differences, i.e., most of the β-diversity at each site resulted from simultaneous gains or losses of species. This pattern could be explained by environmental differences among sites or local disturbances that can benefit some species rather than others (Borcard et al., 2018; Legendre, 2014). On the other hand, differences among two of our sites (BCI and YAS) were almost strictly a result of richness differences. Probably, the antagonism in terms of species richness would explain this pattern. BCI and YAS are exceptional sites because their levels of species richness are among the lowest and highest values, respectively, yet both sites presented higher overall relative species abundance than any other sites. It is interesting to note that even sites with high LCBD values and located within the same region, such as BCI and VB (both in Mesoamerica), were subjected to different processes in terms of mammal community composition. Historical events, such as type and magnitude of habitat fragmentation, the extent of the study areas, and habitat quality, likely promoted different responses from terrestrial mammals and favored a high abundance of some species in BCI but not in VB.

We observed that LCBD values increased from the intact forest landscapes to the fragmented ones, i.e., sites presenting more unique species assemblages were those embedded within fragmented forest landscapes. Such pattern appears to result from a small set of common or dominant species occupying fragmented forests, while continuous forests also harbored generalist species and higher diversity of trophic levels. Indeed, we observed that common species and/or those at low energetic levels (< 3), such as *Dasyprocta* spp., *Cuniculus paca*, and *Pecari tajacu*, were the most abundant species in more spatially restricted landscapes where large-bodied mammals, such as *Tayassu pecari* (white-lipped peccary), *Priodontes maximus* (giant armadillo), *Myrmecophaga tridactyla* (giant anteater), and *Panthera onca* (jaguar) had often been extirpated or highly reduced. A similar pattern was observed for small mammals in Central Amazonian land-bridge islands (Palmeirim et al., 2018), which is comparable to the insular mammal assemblage at BCI.

Analysis accounting for community metrics corroborates our observation above, revealing that LCBD was significantly related to species richness. β- and α-diversity were negatively associated, as we observed at the VB site, which had the highest LCBD value and the lower species richness. These results indicate that mammal communities with fewer species are more uncommon when comparing to the other sites. Similar patterns have been observed for mammals (da Silva et al., 2020; Melo et al., 2009; Ochoa-Ochoa et al., 2014) and other taxonomic groups (Heino and Grönroos, 2017; Landeiro et al., 2018; Legendre and De Cáceres, 2013). In that way, COU, CSN, YAS, and CAX sites presented similar LCBD values, i.e., less variation in their community composition when compared to each other.

On the contrary to our expectations, we did not find a significant relationship between LCBD and relative abundance, functional richness, and functional divergence. This is at odds with a study on small, medium to large-sized, and volant mammals across the Atlantic Forest, which correlated ecologically unique sites with abundance-deficit assemblages and high functional metrics (da Silva et al., 2020). For medium-to-large mammals, these authors observed that LCBD values were negatively related to abundance and functional richness, and positively related to functional divergence, suggesting that LCBD also could be used to predict functional changes in the community (da Silva et al., 2020). However, our results suggest that species losses resulted in greater ecological uniqueness but did not imply lower community abundance and loss of diversity functions, likely due to the high redundancy of functionally related species.

Our results also indicated that the uniqueness of the mammal community was higher in fragmented landscapes presenting low tree basal areas. Tree basal area is a common way to describe the number and size of trees and may represent a gradient of productivity and habitat quality for mammals, while habitat area is a widely recognized determinant of persistence in species with large spatial requirements (Chiarello, 1999; Michalski and Peres, 2007; Pardini et al., 2005; Thornton et al., 2011). In the case of the VB site, the ecological uniqueness could also be affected by the fact that we placed the camera trap stations along a continuous strip of forest spanning a 3000 m altitudinal gradient, which implies important differences in the structure and composition of vegetation and, consequently, in the richness and occupancy of mammal species. (Ahumada, Hurtado, & Lizcano, 2013). Also, fragmentation and habitat modification can result in environmental heterogeneity, which can either favor or inhibit the occurrence and distribution of some mammal species (Michalski and Peres, 2007, 2005; Pardini et al., 2005).

SCBD indices identified species showing high and wide variation in relative abundance across sites, which corroborate previous studies (da Silva et al., 2018; de Paiva et al., 2021; Heino and Grönroos, 2017; Vilmi et al., 2017). For example, *Myoprocta* spp. and *Mazama nemorivaga* were intermediately abundant whenever present but occurred at only four sites. *Tapirus* spp., *Pecari tajacu*, and *Didelphis marsupialis* were recorded at all sites but showed a wide variation in their relative abundances, from rare to relatively common, while *Dasyprocta* spp., *Cuniculus paca*, and *Mazama* spp. were also recorded at all sites and were among the most abundant terrestrial mammals.

Our models reinforced our observations that SCBD values were influenced by species relative abundance but, comparatively, showed a major influence of naïve occupancy, indicating that species exhibiting common to intermediately occupancy levels contributed most to β-diversity, regardless of their functional traits, such as body mass, trophic energy level, activity cycle, or taxonomic group. We observed that *Myoprocta* and *P. tajacu*, species with notably high SCBD, presented similar relative abundance, despite their presence at all sites or not, but are well distributed, occupying between 45 and 60% of the camera trap stations.

Contradicting our prior expectations, our results did not enable us to detect which characteristics could be indicative of species contribution to β-diversity. Nevertheless, most of the important taxa characterizing the variation among sites were species operating at low trophic levels (i.e., herbivores) whereas carnivores contributed less to β-diversity. Beyond differences in landscape structure and protected area sizes, some important points could explain why herbivore abundance was widely variable across sites. We suggest that the co-occurrence (or absence) of apex predators affects herbivore populations through effective top-down control, a well-known mechanism of ecosystem dynamics (Ripple and Beschta, 2012; Terborgh et al., 1999). A previous study comparing three of our eight sites, COU, MAN, and VB, showed a decrease in species richness and occupancy of carnivores along a gradient from continuous to fragmented forest landscapes (Ahumada et al., 2011), which could explain some of the observed variations. Also, herbivorous mammals comprise the most important group of game species in Neotropical forests (Peres, 2000), and hunting pressure was variable across our study sites (Beaudrot et al., 2016), probably impacting some herbivore species.

Studies quantifying SCBD for other taxa also found similar positive relationships with species abundance and occupancy (da Silva et al., 2018; Heino and Grönroos, 2017; Vilmi et al., 2017), which strongly influences this metric (Legendre and De Cáceres, 2013). However, none of the studies using this approach seem to account for any bias resulting from sampling methods and species life history [but see (Krasnov et al., 2019)]. For mammals, for example, sampling methods including either camera trapping or line-transect censuses would be fairly selective (Santos and Mendes-Oliveira, 2012), so surveying strictly terrestrial or arboreal species would require more than one method. In our study, even focusing on ground-dwelling mammals sampled by a single method, it is important to note that species holding small home ranges have a higher detection probability and are recorded more often than wide-ranging species. We highlighted that this study followed the requirements proposed by Legendre (2014), which stated that quantitative indices could be used only when abundance assessments are based on appropriate sampling procedures and are comparable among sites. We believe that standardized and replicable sampling protocols, as adopted in this study, are crucial to obtain reliable results and provide quality information to institutions and government authorities about priority areas for management and conservation.

Our results have direct implications to biodiversity conservation research and planning. However, we note that protected area size is critical, even though this was beyond the original scope of this study, since larger areas are more likely to sustain a greater spectrum of habitat types and a larger set of species with different ecological requirements. As such, habitat area affects the biodiversity metrics explored here, and should be incorporated into the design criteria of similar studies.

5. Conclusions

Our approach using standardizing camera trap monitoring data proved to be effective for a robust assessment of the ecological uniqueness of mammal communities, enabling the identification of species that contributed to current β-diversity patterns. From a biodiversity conservation perspective, monitoring mammal communities through LCBD may provide useful insights to identify changes in community structure from fragmented to continuous forest landscapes, increasing our ability to make forecasts to maximize retention of a complete regional pool of species. We acknowledge that species abundance explains the way β-diversity is partitioned (replacement and richness/abundance difference), but a more detailed analysis about the wide abundance variation observed among sites, whether fragmented and intact (as BCI and YAS, for example), is beyond the scope of this study.

Overall, high LCBD values comprised sites embedded within smaller habitat extents, hosting lower tree basal areas, harboring low species richness, but more ubiquitous and abundant mammal species. Sites within fragmented forest landscapes, like VB, BCI, YAN, and MAN, require rehabilitation and/or actions to mitigate the effects of fragmentation (e.g., ecological corridors, dispersal facilitation), as well as efforts to protect mammals from poachers and other human activities. Even larger protected areas presenting similar levels of ecological uniqueness, such as COU, CSN, CAX, and YAS, should not neglect sustained conservation efforts, including suppression of persistent hunting and wildlife-friendly practices to conserve γ-diversity. In this context, we also emphasize the importance of SCBD, which renders species as feasible ecological indicators, and consequently, conservation efforts can be targeted, for example, to the least ubiquitous or locally rare species. This approach ensures a better understanding of the processes behind β-diversity patterns. We suggest that future studies should focus on assessing whether species contributions to β-diversity can be linked to hunting pressure, habitat disturbance, dispersal limitation, or other factors, to provide additional information to support management of mammal assemblages.

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References

Ahumada, J.A., Hurtado, J., Lizcano, D., 2013. Monitoring the Status and Trends of Tropical Forest Terrestrial Vertebrate Communities from Camera Trap Data: A Tool for Conservation. PLoS One 8, e73707. https://doi.org/10.1371/journal.pone.0073707

Ahumada, J.A., Silva, C.E.F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., McWilliam, A., Mugerwa, B., O’Brien, T., Rovero, F., Sheil, D., Spironello, W.R., Winarni, N., Andelman, S.J., 2011. Community structure and diversity of tropical forest mammals: data from a global camera trap network. Philos. Trans. R. Soc. B Biol. Sci. 366, 2703–2711. https://doi.org/10.1098/rstb.2011.0115

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Beaudrot, L., Ahumada, J.A., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., Eichberg, D., Espinosa, S., Fegraus, E., Fletcher, C., Gajapersad, K., Hallam, C., Hurtado, J., Jansen, P.A., Kumar, A., Larney, E., Lima, M.G.M., Mahony, C., Martin, E.H., McWilliam, A., Mugerwa, B., Ndoundou-Hockemba, M., Razafimahaimodison, J.C., Romero-Saltos, H., Rovero, F., Salvador, J., Santos, F., Sheil, D., Spironello, W.R., Willig, M.R., Winarni, N.L., Zvoleff, A., Andelman, S.J., 2016. Standardized Assessment of Biodiversity Trends in Tropical Forest Protected Areas: The End Is Not in Sight. PLOS Biol. 14. https://doi.org/10.1371/journal.pbio.1002357

Benchimol, M., Peres, C.A., 2015. Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. Biol. Conserv. 187, 61–72. https://doi.org/10.1016/j.biocon.2015.04.005

Bergamin, R.S., Bastazini, V.A.G., Vélez-Martin, E., Debastiani, V., Zanini, K.J., Loyola, R., Müller, S.C., 2017. Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Rainforest. Biodivers. Conserv. 26, 1557–1568. https://doi.org/10.1007/s10531-017-1315-y

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R, Second. ed, Numerical Ecology with R, Use R! Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-71404-2

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R., Shahruddin, W.N., 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim. Conserv. 4, 75–79. https://doi.org/10.1017/S1367943001001081

Chase, J.M., 2003. Community assembly: When should history matter? Oecologia 136, 489–498. https://doi.org/10.1007/s00442-003-1311-7

Chiarello, A.G., 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol. Conserv. 89, 71–82. https://doi.org/10.1016/S0006-3207(98)00130-X

Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. J. Stat. Softw. 34. https://doi.org/10.18637/jss.v034.i02

da Silva, P.G., Bogoni, J.A., Heino, J., 2020. Can taxonomic and functional metrics explain variation in the ecological uniqueness of ecologically-associated animal groups in a modified rainforest? Sci. Total Environ. 708, 135171. https://doi.org/10.1016/j.scitotenv.2019.135171

da Silva, P.G., Hernández, M.I.M., Heino, J., 2018. Disentangling the correlates of species and site contributions to beta diversity in dung beetle assemblages. Divers. Distrib. 24, 1674–1686. https://doi.org/10.1111/ddi.12785

de Paiva, C.K.S., Faria, A.P.J., Calvão, L.B., Juen, L., 2021. The anthropic gradient determines the taxonomic diversity of aquatic insects in Amazonian streams. Hydrobiologia 0123456789. https://doi.org/10.1007/s10750-021-04515-y

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., 2018. Package ‘ adespatial ’ - Multivariate Multiscale Spatial Analysis.

Dray, S., Dufour, A.-B., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. J. Stat. Softw. 22. https://doi.org/10.18637/jss.v022.i04

Earth Explorer, 2017. U.S. Geological Survey [WWW Document]. URL http://earthexplorer.usgs.gov/ (accessed 12.15.18).

Eisenberg, J.F., 1990. Neotropical mammal communities, in: Gentry, A.H. (Ed.), Four Neotropical Rainforests. Yale University Press, New Raven.

Emmons, L.H., Feer, F., 1997. Neotropical Rainforest Mammals: a field guide, 2nd ed. University of Chicago Press, Chicago/London.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1‐km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fox, J., Weisberg, S., 2018. Package “car” - Companion to Applied Regression.

Gaston, K.J., 2000. Global patterns in biodiversity 405, 220–227. https://doi.org/10.1038/35012228

Grass, I., Brandl, R., Botzat, A., Neuschulz, E.L., Farwig, N., 2015. Contrasting taxonomic and phylogenetic diversity responses to forest modifications: Comparisons of taxa and successive plant life stages in south African scarp forest. PLoS One 10, 1–20. https://doi.org/10.1371/journal.pone.0118722

Heino, J., Grönroos, M., 2017. Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia 183, 151–160. https://doi.org/10.1007/s00442-016-3754-7

Heydari, M., Omidipour, R., Abedi, M., Baskin, C., 2017. Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation. Plant Ecol. Evol. 150, 247–256. https://doi.org/10.5091/plecevo.2017.1344

Jansen, P.A., Ahumada, J., Fegraus, E., O'Brien, T.G., 2014. TEAM: A standardised camera-trap survey to monitor terrestrial vertebrate communities in tropical forests, in: Meek, P.D., Fleming, P.J.S. (Eds.), Camera Trapping : Wildlife Management and Research. CSIRO Publishing, Melbourne, Australia, pp. 263–270.

Jetz, W., Fine, P.V.A., 2012. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. PLoS Biol. 10. https://doi.org/10.1371/journal.pbio.1001292

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M., Purvis, A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90, 2648–2648. https://doi.org/10.1890/08-1494.1

Jones, K.E., Safi, K., 2011. Ecology and evolution of mammalian biodiversity. Philos. Trans. R. Soc. B Biol. Sci. 366, 2451–2461. https://doi.org/10.1098/rstb.2011.0090

Kays, R., Arbogast, B.S., Baker- Whatton, M., Beirne, C., Boone, H.M., Bowler, M., Burneo, S.F., Cove, M. V., Ding, P., Espinosa, S., Gonçalves, A.L.S., Hansen, C.P., Jansen, P.A., Kolowski, J.M., Knowles, T.W., Lima, M.G.M., Millspaugh, J., McShea, W.J., Pacifici, K., Parsons, A.W., Pease, B.S., Rovero, F., Santos, F., Schuttler, S.G., Sheil, D., Si, X., Snider, M., Spironello, W.R., 2020. An empirical evaluation of camera trap study design: How many, how long and when? Methods

Ecol. Evol. 11, 700–713. https://doi.org/10.1111/2041-210X.13370

Kerr, J.T., Packer, L., 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385, 252–254. https://doi.org/10.1038/385252a0

Kim, T.N., Bartel, S., Wills, B.D., Landis, D.A., Gratton, C., 2018. Disturbance differentially affects alpha and beta diversity of ants in tallgrass prairies. Ecosphere 9. https://doi.org/10.1002/ecs2.2399

Koleff, P., Lennon, J.J., Gaston, K.J., 2003. Are there latitudinal gradients in species turnover? Glob. Ecol. Biogeogr. 12, 483–498. https://doi.org/10.1046/j.1466-822X.2003.00056.x

Krasnov, B.R., Shenbrot, G.I., Warburton, E.M., van der Mescht, L., Surkova, E.N., Medvedev, S.G., Pechnikova, N., Ermolova, N., Kotti, B.K., Khokhlova, I.S., 2019. Species and site contributions to β -diversity in fleas parasitic on the Palearctic small mammals: ecology, geography and host species composition matter the most. Parasitology 146, 653–661. https://doi.org/10.1017/S0031182018001944

Lacher, T.E., Davidson, A.D., Fleming, T.H., Gómez-Ruiz, E.P., McCracken, G.F., Owen-Smith, N., Peres, C.A., Vander Wall, S.B., 2019. The functional roles of mammals in ecosystems. J. Mammal. 100, 942–964. https://doi.org/10.1093/jmammal/gyy183

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Packag. Version 1.0-12.

Landeiro, V.L., Franz, B., Heino, J., Siqueira, T., Bini, L.M., 2018. Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: Evidence from multiple taxonomic groups. Divers. Distrib. 24, 966–977. https://doi.org/10.1111/ddi.12734

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23, 1324–1334. https://doi.org/10.1111/geb.12207

Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analysing beta diversity: partitioning the spatial variation of community composition data. Ecol. Monogr. 75, 435–450. https://doi.org/10.1890/05-0549

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963. https://doi.org/0.1111/ele.12141

Lennon, J.J., Koleff, P., Greenwood, J.D., Gaston, K.J., 2001. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. J. Anim. Ecol. 70, 966–979. https://doi.org/10.1046/j.0021-8790.2001.00563.x

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P.F., Bellwood, D.R., Mouillot, D., 2012. Quantifying Phylogenetic Beta Diversity: Distinguishing between ‘True’ Turnover of Lineages and Phylogenetic Diversity Gradients. PLoS One 7, e42760. https://doi.org/10.1371/journal.pone.0042760

Li, F., Tonkin, J.D., Haase, P., 2020. Local contribution to beta diversity is negatively linked with community-wide dispersal capacity in stream invertebrate communities. Ecol. Indic. 108, 105715. https://doi.org/10.1016/j.ecolind.2019.105715

Maestri, R., Patterson, B.D., 2016. Patterns of species richness and turnover for the South American rodent fauna. PLoS One 11. https://doi.org/10.1371/journal.pone.0151895

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

Melo, A.S., Rangel, T.F.L.V.B., Diniz-Filho, J.A.F., 2009. Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography (Cop.). 32, 226–236. https://doi.org/10.1111/j.1600-0587.2008.05502.x

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., Mouquet, N., 2011. Beyond taxonomic diversity patterns: How do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob. Ecol. Biogeogr. 20, 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x

Michalski, F., Peres, C.A., 2007. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. Conserv. Biol. 21, 1626–1640. https://doi.org/10.1111/j.1523-1739.2007.00797.x

Michalski, F., Peres, C.A., 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biol. Conserv. 124, 383–396. https://doi.org/10.1016/j.biocon.2005.01.045

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876.

https://doi.org/10.1111/j.1365-2435.2010.01695.x

O'Brien, T.G., 2011. Abundance, Density and Relative Abundance: A Conceptual Framework, in: O'Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer US, New York, pp. 71–96.

Ochoa-Ochoa, L.M., Munguía, M., Lira-Noriega, A., Sánchez-Cordero, V., Flores-Villela, O., Navarro-Sigüenza, A., Rodríguez, P., 2014. Spatial scale and β-diversity of terrestrial vertebrates in Mexico. Rev. Mex. Biodivers. 85, 918–930. https://doi.org/10.7550/rmb.38737

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51, 933–938. https://doi.org/https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Paglia, A.P., Fonseca, G.A.B. da, Rylands, A.B., Herrmann, G., Aguiar, L.M.S., Chiarello, A.G., Leite, Y.L.R., Costa, L.P., Siciliano, S., Kierulff, M.C.M., Mendes, S.L., Tavares, V. da C., Mittermeier, R.A., Patton, J.L., 2012. Lista Anotada dos Mamíferos do Brasil, 2nd ed, Occasional Papers in Conservation Biology. Conservation International, Arlington, VA.

Palmeirim, A.F., Benchimol, M., Morante-Filho, J.C., Vieira, M.V., Peres, C.A., 2018. Ecological correlates of mammal β-diversity in Amazonian land-bridge islands:

from small- to large-bodied species. Divers. Distrib. 24, 1109–1120. https://doi.org/10.1111/ddi.12749

Palmer, M.S., Swanson, A., Kosmala, M., Arnold, T., Packer, C., 2018. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. Afr. J. Ecol. 56, 791–803. https://doi.org/10.1111/aje.12566

Pardini, R., De Souza, S.M., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol. Conserv. 124, 253–266. https://doi.org/10.1016/j.biocon.2005.01.033

Pavoine, S., Vallet, J., Dufour, A.B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. Oikos 118, 391–402. https://doi.org/10.1111/j.1600-0706.2008.16668.x

Peres, C.A., 2000. Effects of Subsistence Hunting on Vertebrate Community Structure in Amazonian Forests. Conserv. Biol. 14, 240–253. https://doi.org/10.1046/j.1523-1739.2000.98485.x

QGIS Development, 2015. QGIS Geographic Information System. Open Source Geospatial Foundation.

Qian, H., 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. J. Syst. Evol. 47, 509–514. https://doi.org/10.1111/j.1759-6831.2009.00043.x

Ricklefs, R.E., 2006. Evolutionary diversification and the origin of the diversity–environment relationship. Ecology 87, 3–13.

https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[3:EDATOO]2.0.CO;2

Ricklefs, R.E., 1987. Community Diversity: Relative Roles of Local and Regional Processes. Science (80-.). 235, 167–171. https://doi.org/10.1126/science.235.4785.167

Ricotta, C., Burrascano, S., 2008. Beta diversity for functional ecology. Preslia 80, 61–71.

Ripple, W.J., Beschta, R.L., 2012. Large predators limit herbivore densities in northern forest ecosystems. Eur. J. Wildl. Res. 58, 733–742. https://doi.org/10.1007/s10344-012-0623-5

Rovero, F., Ahumada, J., Jansen, P.A., Sheil, D., Alvarez, P., Boekee, K., Espinosa, S., Lima, M.G.M., Martin, E.H., O'Brien, T.G., Salvador, J., Santos, F., Rosa, M., Zvoleff, A., Sutherland, C., Tenan, S., 2020. A standardized assessment of forest mammal communities reveals consistent functional composition and vulnerability across the tropics. Ecography (Cop.). 43, 75–84. https://doi.org/10.1111/ecog.04773

Rovero, F., Spitale, D., 2016. Species-level occupancy analysis, in: Rovero, F., Zimmermann, F. (Eds.), Camera Trapping for Wildlife Research. Pelagic Publishing, Exeter, UK, pp. 68–92.

Santos, F., Carbone, C., Wearn, O.R., Rowcliffe, J.M., Espinosa, S., Lima, M.G.M., Ahumada, J.A., Gonçalves, A.L.S., Trevelin, L.C., Alvarez-Loayza, P., Spironello, W.R., Jansen, P.A., Juen, L., Peres, C.A., 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PLoS One 14. https://doi.org/10.1371/journal.pone.0213671

Santos, F., Mendes-Oliveira, A.C., 2012. Diversidade de mamíferos de médio e grande porte da região do rio Urucu, Amazonas, Brasil. Biota Neotrop. 12, 282–291. https://doi.org/10.1590/S1676-06032012000300027

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How Should Beta-Diversity Inform Biodiversity Conservation? Trends Ecol. Evol. 31, 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Stegen, J.C., Hurlbert, A.H., 2011. Inferring Ecological Processes from Taxonomic, Phylogenetic and Functional Trait β-Diversity. PLoS One 6, e20906. https://doi.org/10.1371/journal.pone.0020906

Swenson, N.G., 2011. Phylogenetic Beta Diversity Metrics, Trait Evolution and Inferring the Functional Beta Diversity of Communities. PLoS One 6, e21264. https://doi.org/10.1371/journal.pone.0021264

TEAM Network, 2011. Terrestrial Vertebrate Monitoring Protocol: Implementation Manual, v. 3.1. Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science, Conservation International, Arlington, VA, USA.

TEAM Network, 2010. Vegetation Monitoring Protocol - Implementation Manual. V. 1.5.1, Tropical Ecology, Assessment and Monitoring Network. Center for Applied Biodiversity Science, Conservation International, Arlington, VA, USA.

Team R Core, 2018. R: a language and environment for statistical computing.

Terborgh, J., Estes, J., Paquet, P., Rails, K., Boyd-Heger, D., Miller, B., Noss, R., 1999. The role of top carnivores in regulating terrestrial ecosystems. Cont. Conserv. Sci. Found. Reg. Reserv. Networks 39–64.

Thornton, D.H., Branch, L.C., Sunquist, M.E., Thornton, D.H., Branch, L.C., Sunquist, M.E., 2011. The relative influence of habitat loss and fragmentation : Do tropical mammals meet the temperate paradigm ? Ecol. Appl. 21, 2324–2333. https://doi.org/10.2307/41416658

Urban, M.C., 2015. Accelerating extinction risk from climate change. Science (80-.). 348, 571–573. https://doi.org/10.1126/science.aaa4984

Van Allen, B.G., Rasmussen, N.L., Dibble, C.J., Clay, P.A., Rudolf, V.H.W., 2017. Top predators determine how biodiversity is partitioned across time and space. Ecol. Lett. 20, 1004–1013. https://doi.org/10.1111/ele.12798

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1

Vilmi, A., Karjalainen, S.M., Heino, J., 2017. Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. Divers. Distrib. 23, 1042–1053. https://doi.org/10.1111/ddi.12594

Whittaker, R.H., 1972. Evolution and Measurement of Species Diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. Ecology 95, 2027–2027. https://doi.org/10.1890/13-1917.1

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Fernanda Santos: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing; **Marcela Lima,** ***Santiago Espinosa, Jorge Ahumada, Patrick Jansen, Wilson Spironello, Johana Hurtado:*** Investigation, Data Curation, Writing - Review & Editing; ***Leandro Juen:*** Conceptualization, Methodology, Writing - Review & Editing; ***Carlos Peres:*** Conceptualization, Writing - Original Draft, Writing - Review & Editing.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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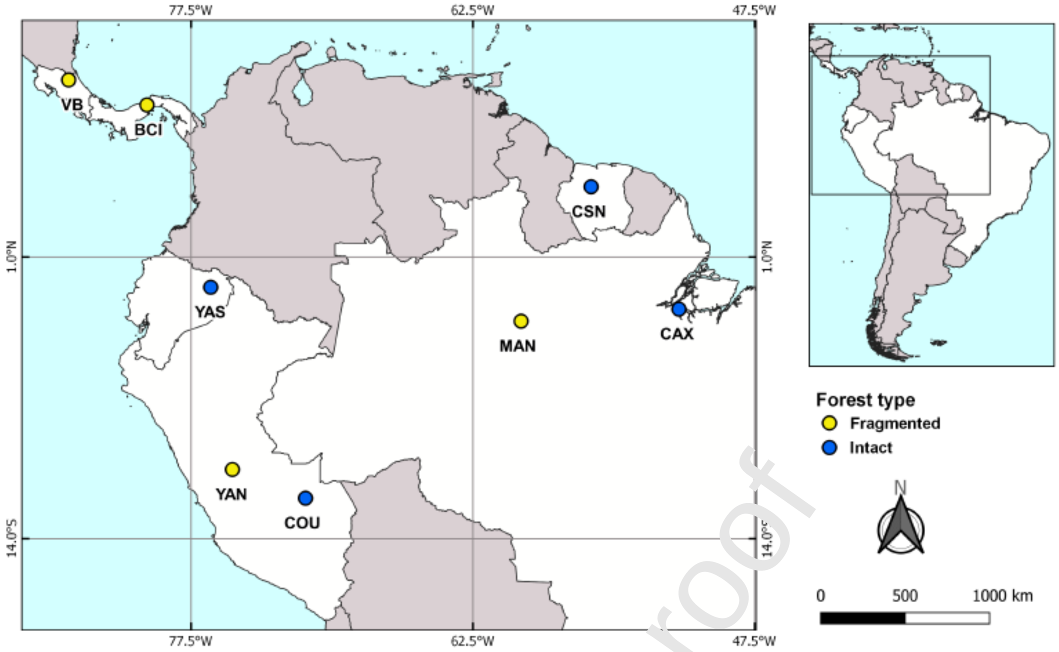


Fig. 1. Location of the eight study sites across Meso and South America: Volcán Barva Transect (VB), Costa Rica; Barro Colorado Nature Monument (BCI), Panamá; Central Suriname Nature Reserve (CSN), Suriname; Yasuni National Park (YAS), Ecuador; Caxiuanã National Forest (CAX), and Manaus (MAN), Brazil; Cocha Cashu – Manu National Park (COU), and Yanachaga National Park (YAN), Peru.

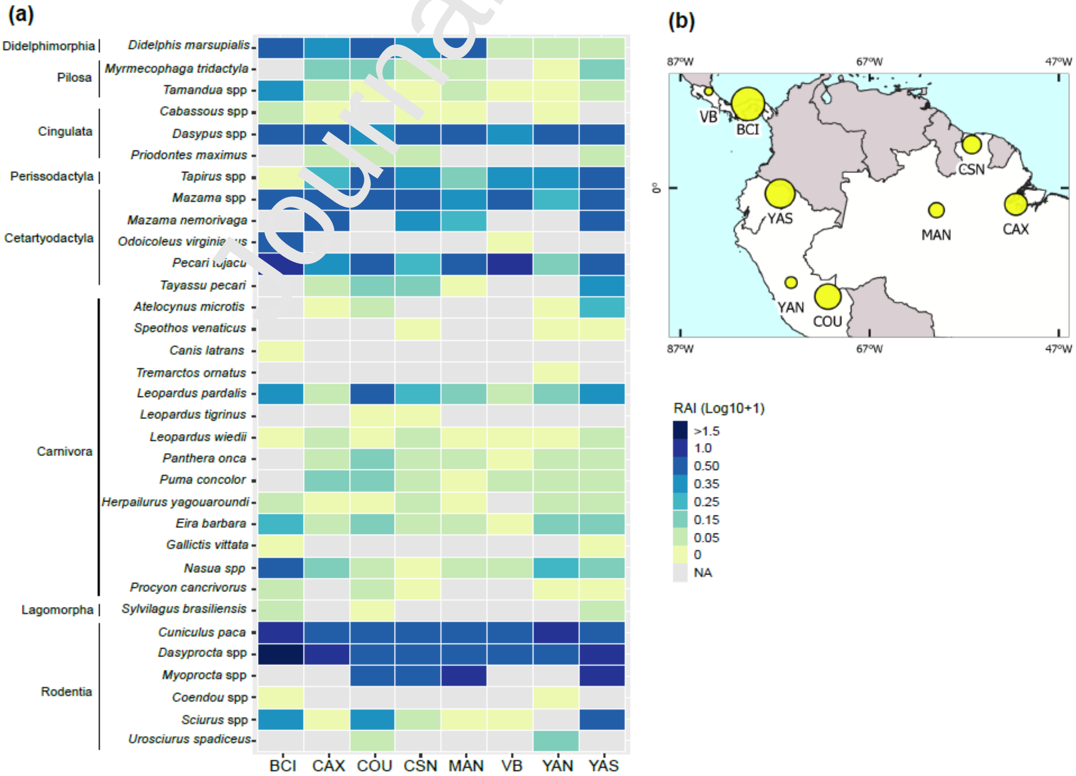


Fig. 2. (a) Species-by-site relative abundance matrix for 33 mammal ecospecies (see definition in the text) surveyed across eight Neotropical forest

sites. Rectangles representing at least one individual recorded per site are colored; Grey rectangles (NA) indicate that species were not recorded; (b) Location map showing comparative total relative abundance of mammal communities for each site. Relative abundance index (RAI) are expressed on a $\log_{10}$ scale.

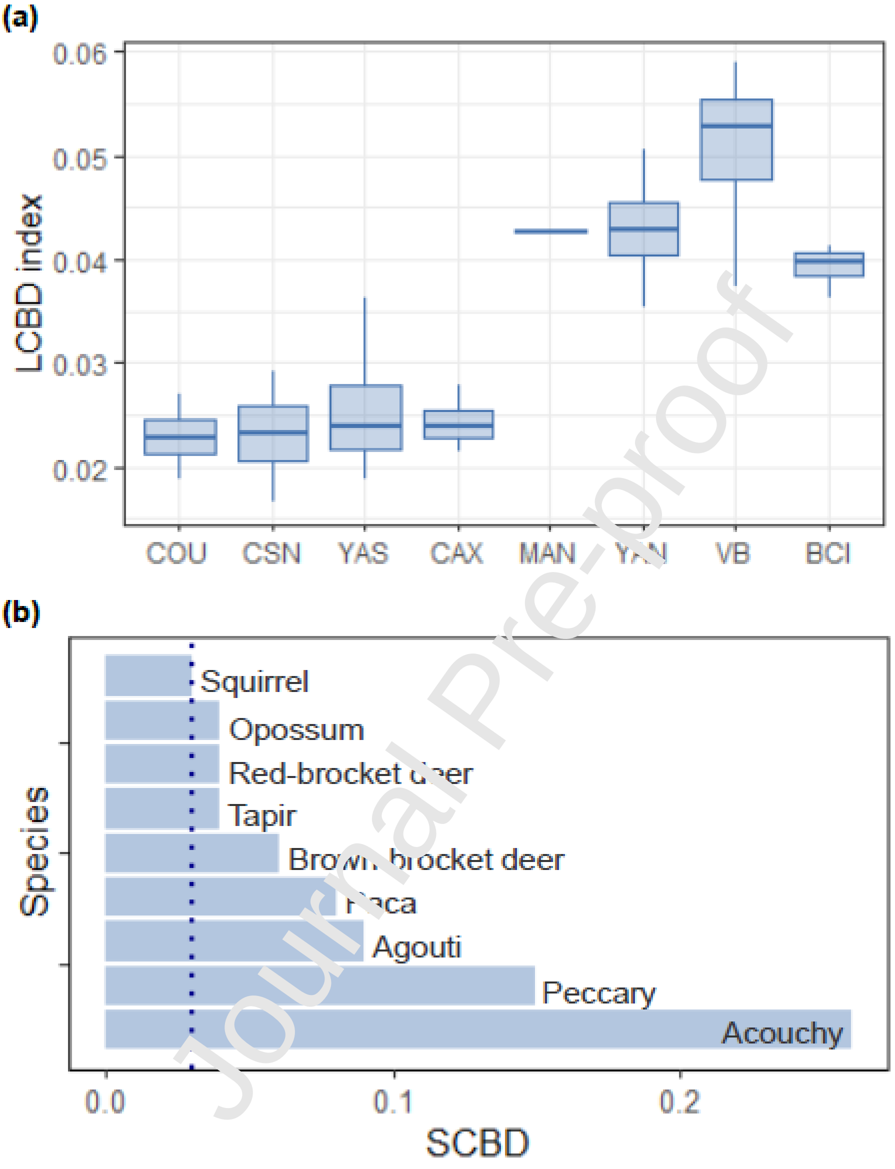


Fig. 3. (a) Difference in local contribution to mammal β-diversity (LCBD) among the eight Neotropical forest sites. Boxes represent interquartile ranges (25% and 75%), solid blue lines within the boxes present median values, and whiskers above and below represent 1.5 times the interquartile range (Study sites ordered from the largest to the smallest study area); (b) Species Contribution to β-diversity (SCBD) of only species with above average values. Dotted line represents the mean value of SCBD.

Fig. 4. β-diversity partitioning of the mammal assemblage at each forest protected area into their species replacement (Repl/yellow) and richness difference (RichDiff/blue) components.

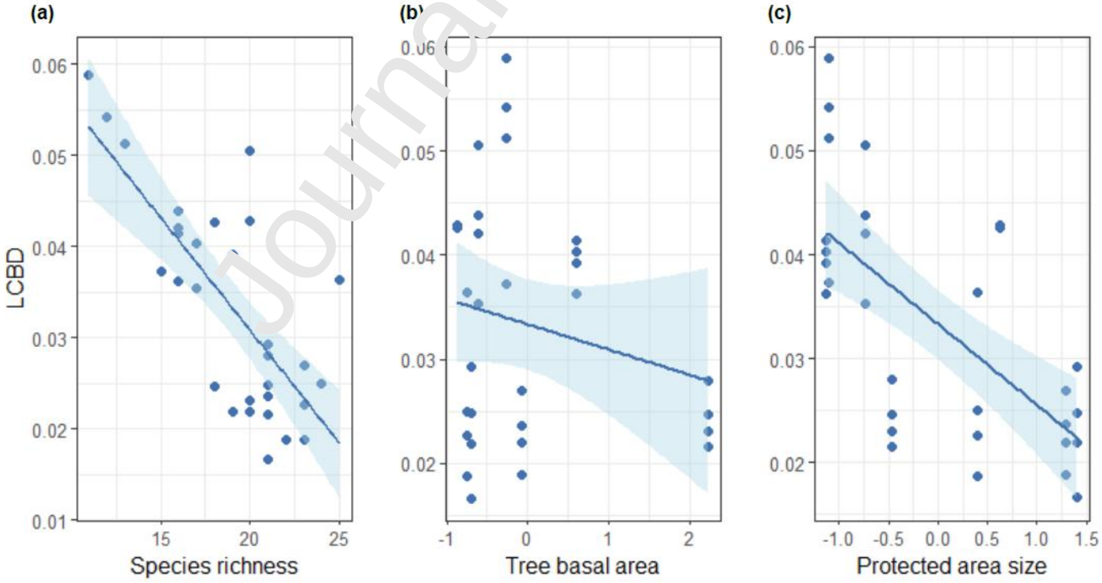


Fig. 5. Relationship between the local site contribution to β-diversity (LCBD) and (a) species richness, (b) tree basal area, and (c) protected area size for Neotropical mammal communities. Shaded blue areas represent the confidence interval of 95% for the linear model.

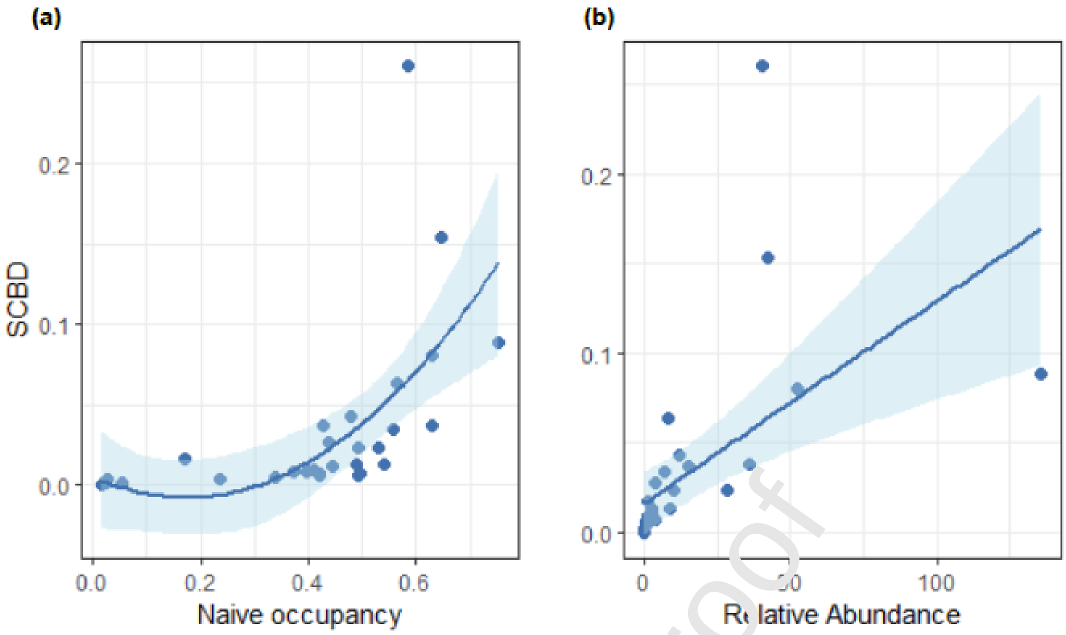


Fig. 6. Relationship between species (a) naive occupancy and (b) relative abundance and Species Contribution to β-diversity (SCBD). Shaded blue areas represent the confidence interval of 95% for the polynomial and linear model, respectively

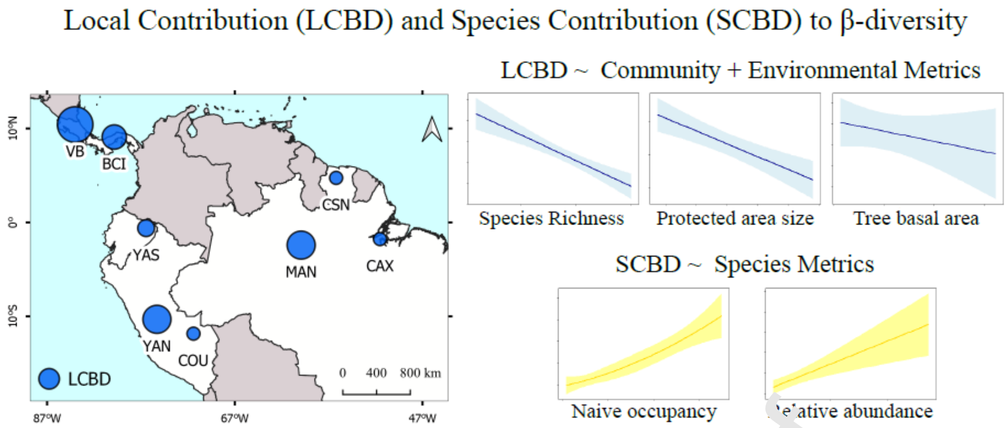
TABLE 1 Results of beta regression analysis explaining LCBD on the basis of either community metrics (Model 1) or environmental variables (Model 2). Asterisks show the level of significance for each variable (*0.001).

	Estimate	**SE**	**z value**	**Model Pseudo R^2**
(1) Community metrics				
(Intercept)	-2.289	0.686	-3.337*	
Species richness	-0.093	0.028	-3.336*	
Relative abundance	0.046	0.043	1.085	
F_{Ric}	8.295	14.283	0.581	
F_{Div}	-0.013	0.625	-0.022	0.526
(2) Environmental variables				
(Intercept)	-3.409	0.036	-95.586*	
Tree basal area	-0.209	0.048	-4.327*	
Protected area size	-0.339	0.041	-8.308*	
NDVI	-0.064	0.039	-1.642	
Precipitation seasonality	0.064	0.045	1.433	0.706

TABLE 2 Results of beta regression analysis when the response variable, SCBD, was explained by either species metrics (Model 1 and 2) or biological traits (Model 3). Asterisks show the level of significance for each variable (*0.001).

	Estimate	**SE**	**z value**	**Model Pseudo-R²**
Model 1				
Intercept	-4.762	0.248	-19.20*	
Naïve occupancy	4.666	0.543	8.59*	0.663
Model 2				
Intercept	-3.565	0.220	-16.205*	
Relative abundance	0.430	0.108	3.951*	0.296
Model 3				
(Intercept)	-3.388	0.837	-4.048*	
Body mass	- 0.022	0.168	-0.131	
Trophic energy level	- 0.197	0.130	-1.510	
Activity cycle	0.156	0.212	0.734	
Order	0.060	0.068	0.884	0.159

Graphical abstract



Highlights

Monitoring data can inform the status of mammal β-diversity at site and species levels

Local contribution to β-diversity (LCBD) describe the ecological uniqueness of a site

Species richness, area size, and tree basal area can predict ecological uniqueness

Species with intermediate to high occupancy contribute more to β-diversity

Ecological uniqueness metrics can guide conservation strategies in protected areas