



The relative importance of forest cover and patch-level drivers for phyllostomid bat communities in the Amazonian Savannas

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Abstract

Context Analyze the multiple dimensions of biodiversity under a local and landscape lens in natural habitats, such as Amazonian savannas, is fundamental for the conservation of species and ecosystems.

Objectives We aim to explore how landscape forest cover and patch-level variables affect the patterns of species abundance, functional traits, and taxonomic, functional and phylogenetic α -diversity of

Phyllostomid bats in forest patches of the Savannas of Amapá, in both the wet and dry seasons.

Methods We used mist nets to survey bats in 26 forest patches. We also quantified forest cover in buffers of 500, 1000, 1500, 2000 and 2500 m around each patch, and tree height, basal area, canopy cover, and vegetation clutter in the understory at the patch level. We used hierarchical partitioning to relate the different indices with our predictor variables.

Results Taxonomic, functional and phylogenetic diversity in the wet season increased with the proportion of forest cover in the 2500 m buffer. Vegetation clutter was negatively related to taxonomic and

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functional diversity in the wet season. In the dry season, average tree height positively affected taxonomic and functional diversity. Patch-level variables were more important than forest cover in explaining the average functional traits in both seasons.

Conclusion We found seasonal variation in the relationships between components of bat diversity and different drivers. Since both forest cover in the landscape and patch-level variables are important for Phyllostomid bat diversity, conservation plans should consider forest conservation at the landscape level and maintenance of forest patch quality.

Keywords Chiroptera · Functional diversity · Habitat amount · Phylogenetic diversity · Seasonality · Tropical savannas

Introduction

Environmental heterogeneity, due to variation in local and landscape level factors, is one of the key drivers of patterns of biodiversity and species habitat use (Stein et al. 2014). However, local and landscape variables can act differently upon different components of biodiversity, such as diversity and species composition, and on different taxonomic groups (Cisneros et al. 2015; Mendes et al. 2017; Calle-Rendón et al. 2020; Fuentes-Montemayor et al. 2020). One key way in which these variables act to shape species and assemblage responses is through the provision of trophic resources (e.g., fruits and insects) and shelter. This leads to environment filtering, with animal responses varying depending on species functional traits (e.g., trophic guild and dispersal capacity - With 1994; Weiher and Keddy 1995). Given the important impacts of rainfall and temperature on the availability and seasonality of trophic resources (Ramos Pereira et al. 2010a), species may also be expected to use different habitats in distinct ways, or for contrasting purposes, in different seasons of the year (Cisneros et al. 2015).

In tropical forests, vertebrate diversity is in part driven by local variables, such as tree height and density, canopy cover and vegetation clutter (Roll et al. 2015; Bobrowiec and Tavares 2017; Calle-Rendón et al. 2020). However, at the landscape-scale proportional forest area is one of the key drivers of animal species diversity in tropical forests (Melo et al.

2017; Mendes et al. 2017; Calle-Rendón et al. 2020). Indeed, the Habitat Amount Hypothesis (HAH) predicts that species density and richness should be higher in sites surrounded by more habitat cover (Fahrig 2013). As such, even small forest patches can present levels of richness and density that are quite similar to nearby larger patches if forest cover in the surrounding landscape is sufficiently high (Fahrig 2013). The HAH has been tested in different anthropogenically fragmented landscapes (Melo et al. 2017; Vieira et al. 2018), but should also be expected to hold up for naturally patchy ecosystems, such as the Amazonian Savannas. The Amazonian Savannas are excellent natural laboratories for both ecological and conservation studies (e.g., Rosa et al. 2021). They consist of highly heterogeneous landscapes, made up of different and highly contrasting habitat types (Mustin et al. 2017), and as such they serve as excellent study areas to investigate the influence of landscape structure and composition, including forest cover, on different components of biodiversity (Bernard and Fenton 2007; Calle-Rendón et al. 2020).

In the Amazonian Savannas, taxonomic, functional and phylogenetic diversity of bats have been shown to be higher in forest patches than in the savanna matrix, and bat abundance and diversity to be higher in the wet season (Carvalho et al. 2018; Carvalho et al. 2021). The savanna matrix is permeable for bats and other more mobile species, which use this habitat to fly between forest patches and between patches and adjacent areas of continuous forest (Bernard and Fenton 2003; Loayza and Loiselle 2009; Carvalho et al. 2021). However, there is still a large knowledge gap concerning how bats use the different habitats that make up these naturally patchy ecosystems (Bernard et al. 2011; Carvalho and Mustin 2017), and few studies have tried to elucidate how local and landscape level variables act to determine patterns of bat diversity throughout the neotropical savannas, such as the Amazonian Savannas (e.g., Mendes et al. 2017). Of those studies that have been carried out in Amazonian Savannas, most have focused exclusively on the taxonomic dimension of diversity, leaving out the functional and phylogenetic dimensions (Bernard et al. 2011; Carvalho and Mustin 2017). Functional diversity is based on functional traits (characteristics of species that can be measured or categorized) and predict ecosystem functioning more precisely (Tilman 2001). Phylogenetic diversity measures the

biodiversity based on branch lengths of a phylogeny, predicting, for example, the shortest path to the most recent common ancestor of a group of species (Faith 1992; Faith 2018). Therefore, studying the different dimensions of diversity together can provide more robust answers to ecological questions, such as those related to landscape factors that affect bats (Cisneros et al. 2015), as well as having direct implications for species and habitat conservation (Faith 2018; Freitas and Montovani 2018).

To date, no studies have investigated how local and/or landscape drivers affect species and functional traits of phyllostomid bats in Amazonian Savannas. Our current knowledge is based on studies carried out in other Amazonian ecosystems (e.g., *terra firme* forest) or in anthropogenically fragmented areas (e.g., Marciente et al. 2015; Rocha et al. 2017; Farneda et al. 2018). For example, phytophagous bats (frugivorous and nectarivorous – e.g., *Uroderma bilobatum* and *Glossophaga soricina*, respectively) are negatively affected, and animalivorous bats (insectivores and carnivores – e.g., *Gardnerycteris crenulatum* and *Trachops cirrhosus*, respectively) are positively affected, by vegetation cover (e.g., Rocha et al. 2017; Farneda et al. 2018). These patterns are mainly related to the availability of food for each of these trophic levels, which tends to be, for example, higher for animalivorous bats in areas with higher vegetation cover (Meyer et al. 2016; Rocha et al. 2017; Farneda et al. 2018). Aspect ratio and wing loading have also been shown to be important drivers of habitat use by bats, with bats that have higher values for these functional traits (e.g., *Artibeus planirostris*) more frequently using environments with fewer obstacles (less vegetation cluttering) than do those bats that have lower values (e.g., *Lophostoma silvicola*-Marinello and Bernard 2014; Bobrowiec and Tavares 2017).

Here, we aim to explore the relative importance of proportional forest cover in the landscape and different patch-level characteristics (canopy cover, vegetation clutter or density of understory vegetation, and tree height and basal area) on species, functional traits, and taxonomic, functional and phylogenetic α -diversity of Phyllostomid bats. To do so, we captured bats in 26 different forest patches of the Savannas of Amapá, in the northeast of the Brazilian Amazon, in both the wet and dry seasons. Specifically, we expect to find that both landscape forest cover and patch-level characteristics will be important drivers of

overall patterns of bat diversity. However, we expect that landscape forest cover will be more important than patch-level drivers, as supported by the Habitat Amount Hypothesis (HAH-Fahrig 2013). We further expect that functional traits associated with mobility, such as aspect ratio and wing loading (Norberg 1994; Marinello and Bernard 2014), will be associated positively with landscape level forest cover. In contrast, we expect that the relative weight of functional traits related to trophic level and diet will be much more driven by patch-level characteristics. Specifically, we predict that phytophagous (frugivorous and nectarivorous), as well as omnivorous species, will be more associated with forest patches where canopy cover and tree height are lower, tending to have understory with higher density of pioneer plants and offer more fruits and flowers for more generalist bat species (Meyer et al. 2016; Farneda et al. 2018). Conversely, we expect that animalivorous (insectivorous and carnivorous) species will be more associated with areas with higher canopy cover and taller trees, as habitats with these characteristics tend to have a greater availability of animal prey (Meyer et al. 2016; Farneda et al. 2018). Finally, we expect that the patch-level abundance of the most captured species will follow the same patterns expected for their respective functional traits, particularly trophic guild and diet.

Methods

Study area

This study was carried out in the southeastern region of the Savannas of Amapá, in the northeast of the Brazilian Amazon (Fig. 1). The study area is part of a unique Amazonian ecosystem type, known as Amazonian savanna, which is currently highly threatened by diverse anthropogenic actions (Carvalho and Mustin 2017; Mustin et al. 2017). These ecosystems are characterized by a mosaic of forest patches, wetlands and *buritizais* (monodominant gallery forest of *Mauritia flexuosa*), spread across a wide savanna matrix (Mustin et al. 2017). Over the last 30 years, increasing land-use change has occurred in the Savannas of Amapá, particularly due to plantations of soybeans and eucalyptus, as well as large, uncontrolled forest fires (Mustin et al. 2017; Carvalho et al. 2019a).

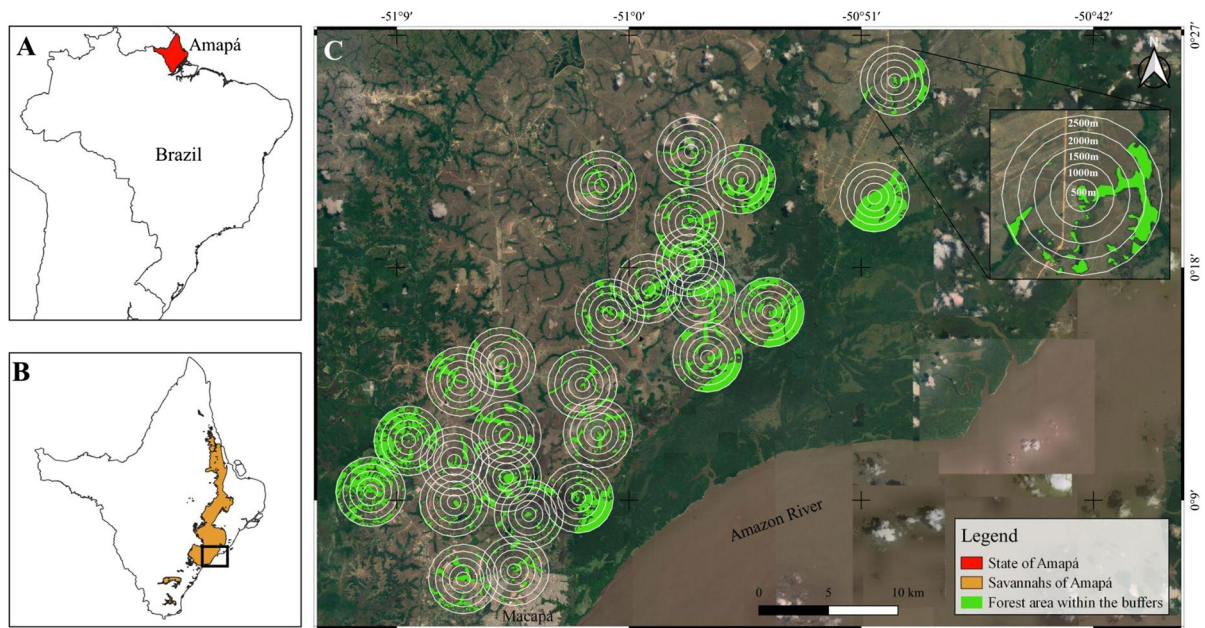


Fig. 1 Brazil with the state of Amapá, in the northeast of the Brazilian Amazon, highlighted in red (A). Distribution of the Savannas of Amapá throughout the state of Amapá, with the study area highlighted by the black box (B). Distribution of the

26 forest patches in which bats were sampled (C). The buffers around each sampling site have radii of 500–2500 m in 500 m increments

The Savannas of Amapá are characterized by a monsoon tropical climate (Am in the Köppen classification). The wet season, from December to July, is characterized by months with rainfall above 100 mm, and the dry season runs from August to November (Tavares 2014). The temperature does not vary widely throughout the year, and is on average 27 °C (Tavares 2014).

Sampling design

Twenty-six forest patches were selected throughout the study area, with a minimum distance of 2.5 km between sampled patches. This minimum distance was used to increase the spatial independence of the sampling sites, as some bat species (e.g., *Artibeus* spp.) have been shown to move 0.2–5.6 km in a single night in areas of Amazonian savanna (Bernard and Fenton 2003). Phyllostomid bats were captured with mist nets set along a ~110 m long transect set at least 30 m from the edge of each forest patch. Thirty meters was considered sufficient as the smallest natural patch sampled had a width of approximately 100 m. The patches were chosen based on accessibility (by roads

or trails), and to encompass different amounts of forest cover in a 2.5 km radius around the center of each transect. All forest patches sampled were surrounded by a matrix of park savanna (Mustin et al. 2017), which is characterized by an open canopy and trees no taller than 2 m (Costa-Neto 2014). Furthermore, all the patches were transected by rivers or adjacent to temporary or permanent bodies of water, with the former being flooded in the wet season only.

Sampling of bats

Between August 2016 and January 2020, nine mist-nets (12 × 3 m; 14 mm mesh size) were used to sample bats along each transect during four nights (two nights each in the wet and dry seasons; one transect per sampled patch). The mist-nets were opened at sunset and left open for six hours each night. To avoid bias in capture rates due to bats learning the position of the nets and subsequently avoiding them, either a minimum interval of 30 days between samplings was used (15 patches), or sampling was on consecutive nights in each season, but the mist nets were relocated within the patch at least 50 m from the previous

position (11 patches - Marques et al. 2013). We subsequently tested for any difference between the two sampling methods for all variables, and none was found (t -test p -values > 0.05).

Forest cover

Forest cover was quantified in buffers of 500, 1000, 1500, 2000 and 2500 m around each transect, using the landscape classification available via MapBiomias Brazil (<https://mapbiomas.org/en>). The classified images of the whole study area were downloaded from MapBiomias for the year 2018, and were then vectorized using QGIS (version 3.16 - QGIS Development Team 2021). These shapefiles were then corrected for mis-classification of wetland areas using a shapefile downloaded from Global Wetlands (<https://www2.cifor.org/global-wetlands/>). Using the corrected shapefile and the software QGIS, we selected only the forest components of the study area and then quantified the proportional forest cover in each buffer. This final classification was compared with Google Earth images and was found to consistently correctly classify the forest patches. After subsequent checking, proportional forest cover was found to be highly (> 0.8) correlated between most buffer levels, with only levels of 500 and 2500 m showing a low-level of correlation (< 0.5). As such, only these two buffer sizes were used in subsequent analyses. The average forest cover (\pm standard deviation) was 4.27 ± 2.48 km² for the 2500 m buffers and 0.26 ± 0.03 km² for the 500 m buffers (Supplementary Information 1 – Table A1).

Patch-level variables

The height of all trees and shrubs with a diameter at breast height (DBH) of ≥ 10 mm was estimated using a Laser Range Finder (AOMASO® HT-60) in a 100×2 m transect (Supplementary Information 1 – Table A1). The transect was established running parallel to the mist-net transect, but at a distance of at least 1 m, to minimize the effect of vegetation removal during mist net set-up. Subsequently, average tree height in each forest patch was calculated based on these data. We estimated the basal area of each tree by the equation $D^2\pi/4$, in which D is the tree diameter. Subsequently, the basal area of each transect was estimated by the sum of the basal area of all

trees. In order to estimate canopy cover, a photograph was taken with a smartphone and a fisheye lens every 25 m (i.e., 0 m, 25 m, 50 m, 75 and 100 m) along each transect with the smartphone positioned at a height of ~ 2 m above ground level and pointing vertically to the canopy. For each photograph, we then calculated a leaf area index that varies between 0 and 100%, using the “Gap Light Analysis Mobile App” - GLAMA (Tichý 2016). Average canopy cover for each transect was then calculated by taking the average of the five photographs. The intercept point sampling method was used to estimate vegetation clutter in the understorey (Dias-Terceiro et al. 2015). For this method, a 1.5 m long cane was held vertically 50 cm above ground level whilst walking the length of each transect, at a distance of one meter from the center of the transect, and the number of direct contacts between the cane and any foliage or branches was quantified. As such, vegetation clutter for each forest patch was calculated as the total number of contacts between the cane and the vegetation along the length of the transect (Supplementary Information 1 – Table A1). To minimize differences in accuracy of the patch-level variable estimates, for the eleven patches in which bats were sampled on subsequent nights along two different transects, patch-level variables were estimated using the data collected along the first half of each transect.

Functional traits and phylogeny

For the estimates of functional diversity, we used functional traits which are directly associated with forest use by phyllostomid bats (e.g., Farneda et al. 2018; Carvalho et al. 2021-Supplementary Information 1–Table A2), specifically: wing attributes (aspect ratio and wing loading), body mass, use of the forest vertical stratum (canopy and understorey), trophic level (animalivorous and phytophagous), and diet (frugivores, insectivores, nectarivores, omnivores, carnivores, and sanguinivores). For aspect ratio and wing loading, we used data from Tavares (2013) and Marinello and Bernard (2014). Values of body mass for each individual were obtained in the field using spring scales, and an average for each species was subsequently calculated, based solely on the data for adult males, as females could be pregnant, even when no foetus could be palpated (Carvalho et al. 2019b). The bat species were classified in terms of vertical

stratification within the forest as either understory or canopy species (Bernard 2001; Kalko and Handley 2001; Ramos Pereira et al. 2010b). The bats were classified in animalivorous or phytophagous (trophic level) following Giannini and Kalko (2004). Diet was classified based on the Ecological Register database (<http://ecoregister.org/>), which includes a repository of published papers from around the world (Alroy 2017). For the estimates of phylogenetic diversity, we used an up-to-date phylogenetic tree for Chiroptera (Upham et al. 2019).

Data analysis

Alpha diversity

Taxonomic, functional and phylogenetic diversities were estimated based on Hill numbers (Chao et al. 2014). Hill numbers are defined by the q parameter, which takes into account the weight given to relative species abundances in the calculation of diversity estimates, such that they are less sensitive to the presence of rare species as the q number increases (Hill 1973; Chiu and Chao 2014). Here, we used q values that represent species richness ($q=0$, where species abundances are ignored), Shannon diversity ($q=1$, where all species are weighted by their relative abundances), and Simpson diversity ($q=2$, where common species receive greater weight than rare species; Hill 1973; Chiu and Chao 2014). All Hill numbers were estimated using the R package “hillR” (Li 2018). For functional richness and diversity, the Hill numbers incorporated a functional distance matrix constructed based on the species’ functional traits (see Chiu and Chao 2014). For phylogenetic richness and diversity, the Hill numbers incorporated the phylogenetic tree (Li 2018).

Community weighted mean

The use of indices weighted by relative abundances allows for changes in the average values of species traits between assemblages to be calculated (Lavorel et al. 2008). In order to do so, here we used the community weighted mean (CWM), which is the average value of functional traits weighted by the relative abundances of the species in each sampled forest patch (Lavorel et al. 2008). CWM was

estimated using the R package ‘BAT’ (Cardoso et al. 2021).

Relative importance of the proportional forest cover and patch-level variables on phyllostomid bat diversity and abundance.

The independent contribution of proportional forest cover (in buffers of 500 and 2500 m), and of the patch-level variables (tree height, basal area, canopy cover, and vegetation clutter - Supplementary Information 1 – A1) to each of the estimated diversity indices, CWM and species abundance in each season (wet and dry-Supplementary Information 1–A3 to A8) was estimated using hierarchical partitioning (Chevan and Sutherland 1991; Cisneros et al. 2015), implemented using the R package ‘hier.part’ (Walsh and Nally 2020). Beyond reducing problems of collinearity, hierarchical partitioning allows for the estimation of the independent contribution (I) of each explanatory variable, separately from the contribution of the variables as a set (J) (Chevan and Sutherland 1991). Given that running multiple tests can increase the likelihood of type I errors (Gordon et al. 2007), we adjusted the critical value (α) to 0.001 (Bonferroni adjustment approach; Gordon et al. 2007), taking into account all 58 models that were run. We also confirmed the absence of spatial auto-correlation for all response variables using the Moran’s I of the residuals of all models. All mentioned packages were loaded in Program R (R Core Team 2021).

Results

A total of 1666 bats were captured, of which 1000 were captured in the wet season and 666 in the dry season (Supplementary Information 1–Table A9). Nine species had at least 50 individuals captured, including: *Carollia perspicillata* (440 captures), *Artibeus planirostris* (321 captures), *Lophostoma silvicolu* (135 captures), *Gardnerycteris crenulatum* (92 captures), *Artibeus cinereus* (86 captures), *Artibeus lituratus* (68 captures), *Artibeus obscurus* (68 captures), *Uroderma bilobatum* (53 captures), and *Rhinophylla pumilio* (51 captures).

In the wet season, proportional forest cover in the 2500 m buffer was the most important variable in explaining patch differences in all diversity dimensions, with taxonomic, functional and phylogenetic diversity increasing with increasing proportional

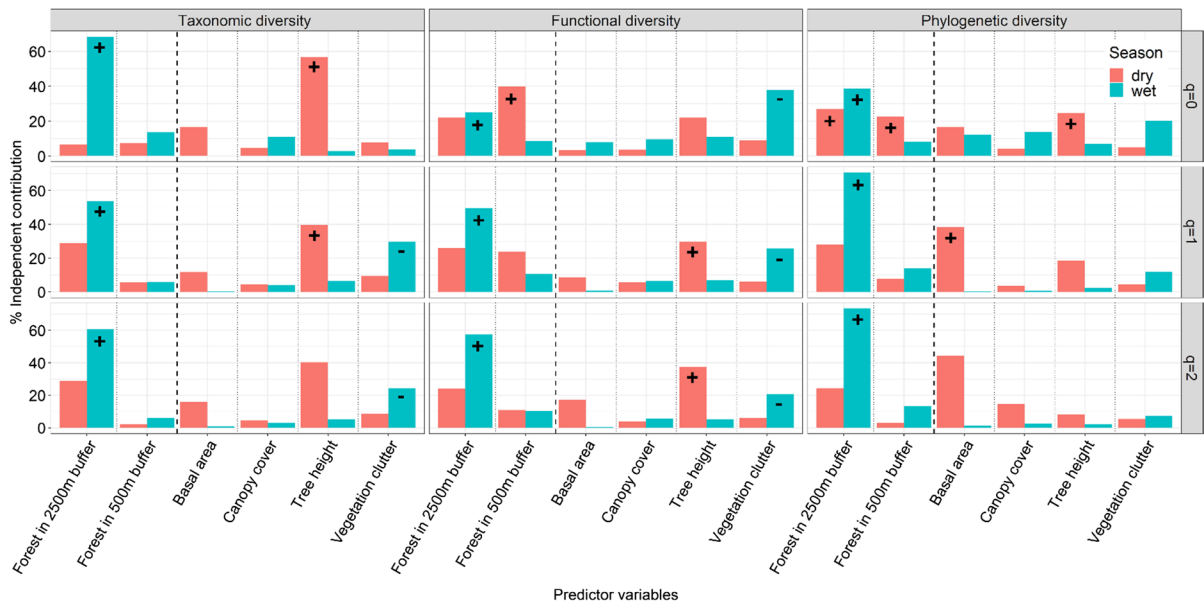


Fig. 2 Proportional independent contribution of the landscape forest cover and patch-level variables to each of the dimensions (taxonomic, functional and phylogenetic) of bat diversity, for each of the estimated Hill numbers ($q = 0, q = 1, q = 2$), in each season (wet and dry), derived from hierarchical partition-

ing. The vertical dashed line indicates the separation between the two forest cover variables (left) and the four patch-level variables (right). Significant results are indicated with a plus (for positive effects) or minus (for negative effects) sign

forest cover (Fig. 2). Vegetation clutter at the patch-level was also an important factor in explaining taxonomic and functional diversity in each patch in the wet season, with both being lower where vegetation clutter was higher (Fig. 2). In the dry season, average tree height was the most important variable, with taxonomic and phylogenetic richness and taxonomic and functional diversity increasing with tree height. However, proportional forest cover in the 500 m buffer also had an important positive influence on functional and phylogenetic richness, and proportional forest cover in the 2500 m buffer on phylogenetic richness. Also, the basal area had a positive influence on phylogenetic diversity. The other explanatory variables were not significantly important in explaining any of the dimensions of diversity (Fig. 2; Supplementary Information 2).

Patch-level variables were more important than proportional forest cover in explaining community weighted means in both the wet and the dry seasons (Fig. 3). In the wet season, canopy cover was the most important variable in explaining community weighted means, having a positive effect on both insectivorous diets and the animalivorous trophic level, and a

negative effect on frugivorous diets and the phytophagous trophic level (Fig. 3). Body mass also declined with increasing vegetation clutter. At the landscape level, proportional forest cover at 500 m had a positive effect on the animalivorous and a negative effect on the phytophagous trophic levels (Fig. 3; Supplementary Information 2).

In the dry season, forest cover at 2500 m, canopy cover, vegetation clutter, tree height and basal area were the most important variables for explaining the differences in community weighted means (Fig. 3). Proportional forest cover in the 2500 m buffer had a positive effect on omnivorous diets. Canopy cover had a positive effect on insectivorous diets and a negative effect on wing aspect, and vegetation clutter had a positive effect on the animalivorous and a negative effect on the phytophagous trophic levels. Tree height had a positive effect on carnivores, while basal area had a negative effect on frugivorous diets, and body mass declined with vegetation clutter (Fig. 3; Supplementary Information 2).

Of the most-captured species, only the abundances of *A. lituratus*, *C. perspicillata* and *L. silvicola* were not influenced by the explanatory variables (Fig. 4).

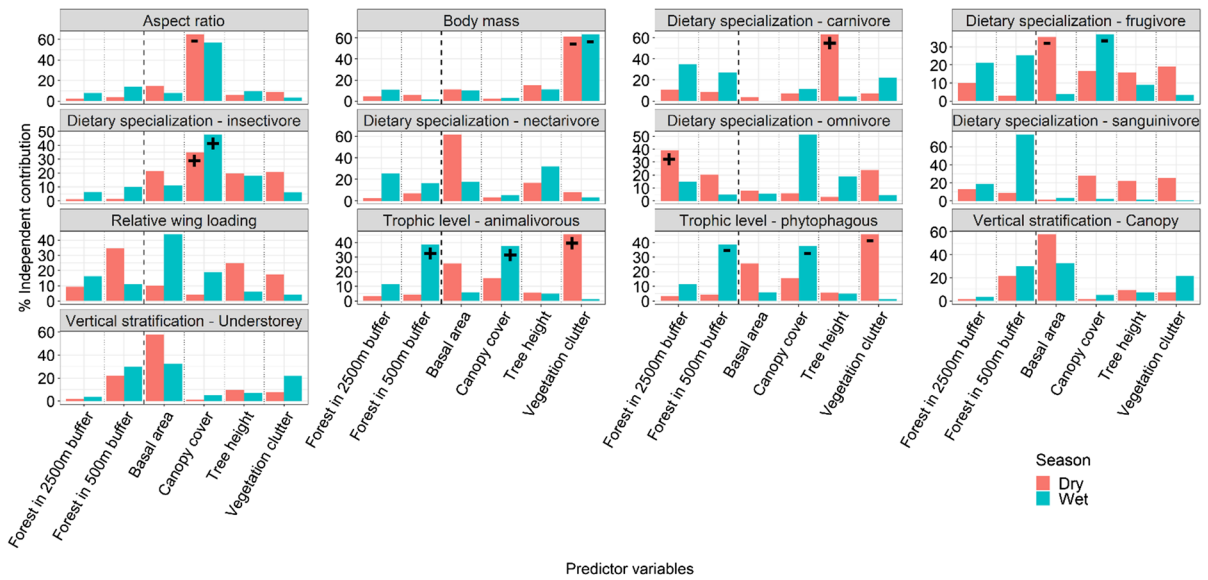


Fig. 3 Proportional independent contribution of the landscape forest cover and patch-level variables to each of the different community weighted means, in each season (wet and dry), derived from hierarchical partitioning. The vertical dashed line

indicates the separation between the two forest cover variables (left) and the four patch-level variables (right). Significant results are indicated with a plus (for positive effects) or minus (for negative effects) sign

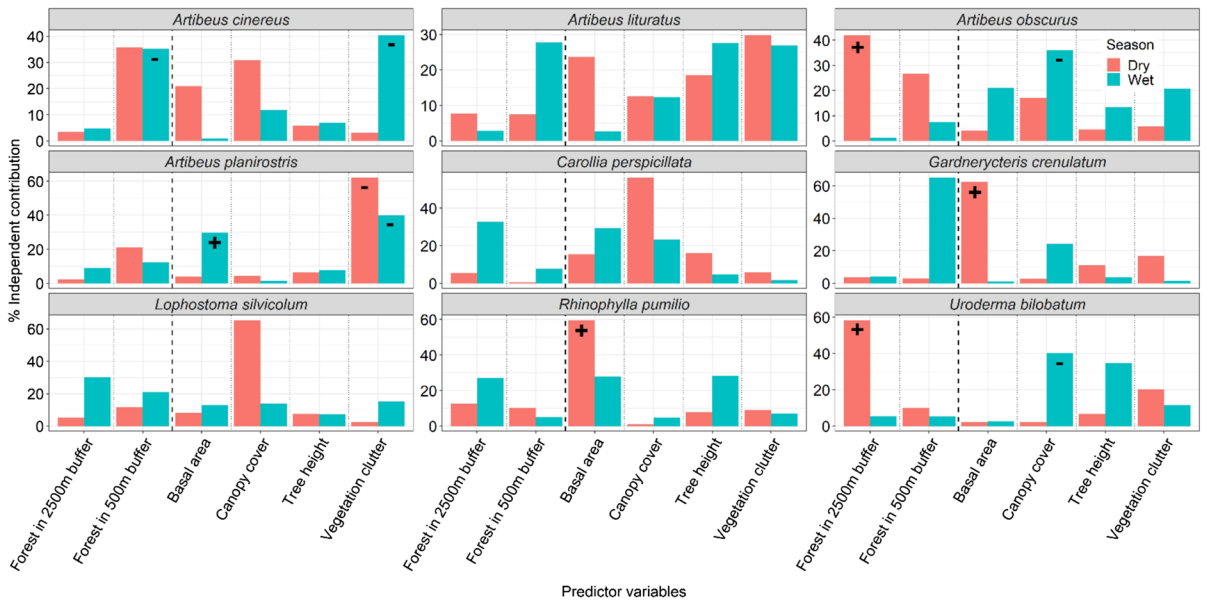


Fig. 4 Proportional independent contribution of the landscape forest cover and patch-level variables to the abundances of the most-captured phyllostomid bat species, in each season (wet and dry), derived from hierarchical partitioning. The

vertical dashed line indicates the separation between the two forest cover variables (left) and the four patch-level variables (right). Significant results are indicated with a plus (for positive effects) or minus (for negative effects) sign

The abundance of *G. crenulatum* and *R. pumilio* increased with basal area in the dry season, whereas

that of *A. obscurus* and *U. bilobatum* decreased with canopy cover in the wet season and increased with

forest cover in the 2500 m buffer in the dry season. The abundance of *A. cinereus* and *A. planirostris* decreased with vegetation clutter in the wet season. Also, the abundance of *A. cinereus* was negatively affected by forest cover in the 500 m buffer in the wet season, and the abundance of *A. planirostris* was negatively affected by vegetation clutter in the dry season and positively by basal area in the wet season (Fig. 4; Supplementary Information 2).

Discussion

The results of this study show that both landscape-level forest cover and patch-level drivers are important determinants of taxonomic, functional and phylogenetic diversity of understory phyllostomid bats in forest patches of the Savannas of Amapá, relationships that are maintained for different weights of relative species abundance on diversity indices. However, we found seasonal differences in the relative importance of these factors for overall diversity, with landscape-level factors most important in the wet season, and patch-level factors in the dry season. Taken together, these results show that the maintenance of diverse (in terms of both species and lineages) and functional bat assemblages in forest patches in the Amazonian Savannas depends on both characteristics of the forest patches themselves and of the forest amount in the landscape. This has important implications for effective conservation of the Amazonian Savannas and their bat diversity, suggesting that a combination of forest conservation and restoration at the landscape level and maintenance and restoration of forest patch quality are required, in addition to protection of the savanna matrix.

Studies carried out in fragmented landscapes throughout the Amazon biome have shown that there is a loss of bat species, functions and lineages as landscape-level forest cover declines (Rocha et al. 2017; Farneda et al. 2018; Aninta et al. 2019). Here, we show that landscape-level forest cover is similarly important for all dimensions of bat diversity within forest patches in this naturally patchy Amazonian landscape that has evolved over thousands of years (Silva and Bates 2002). Our results show that in the wet season, taxonomic, functional and phylogenetic richness and diversity of phyllostomid bats increase with increasing proportional forest cover in

a buffer of 2500 m, regardless of the weight given to relative species abundances, in line with the Habitat Amount Hypothesis (Fahrig 2013) and our expectations. Indeed, forest cover in the 2500 m buffer was the most important variable explaining differences in diversity between patches in the wet season, because areas with higher proportional forest cover offer more usable space for most bat species to find resources (i.e., food and shelter – Mendes et al. 2017). Given the importance of landscape-level forest cover for phyllostomid bat diversity, conservation strategies in the Savannas of Amapá should include measures to preserve and restore forest cover that has been lost to anthropogenic disturbances.

However, management of landscape-scale forest cover cannot be the sole strategy in these naturally patchy landscapes. Contrary to our expectations, in the dry season the positive effect of landscape level forest cover (in a buffer of 500 m) persists only for functional and phylogenetic richness, and for the abundance of two of the most captured species, *A. obscurus* and *U. bilobatum*. In this season, tree height at the patch level is the most important determinant of taxonomic richness and diversity and of functional diversity and phylogenetic richness. This reflects the tendency for forest patches with taller trees to be more mature and more highly structured than those with smaller trees, increasing the availability of resources (see Supplementary Information 3) for different species and, consequently, the number of niches available (Peña-Claros 2003; Vleut et al. 2013; Martins et al. 2017). In the Savannas of Amapá, the forest patches with taller trees mainly occur closer to permanent water bodies (close to large streams or rivers). We would suggest that the absence of a relationship between bat diversity and tree height in the wet season then reflects the higher availability of resources more generally at this time of year, with resource limitation in the dry season concentrating bats into those forest patches with taller trees, which have greater availability of water and resources (see Supplementary Information 3).

However, even in the wet season, patch level vegetation clutter has important impacts on bat diversity, with both taxonomic and functional diversity, and functional richness, declining with increasing clutter, as we had predicted. Previous studies have shown similar negative effects of vegetation clutter on species and guild richness and abundance of

phyllostomid bats in the Amazon (Marciente et al. 2015; Bobrowiec and Tavares 2017). The negative effects of vegetation clutter are also related to forest structure, in the sense that more open understoreys allow for easier movement and as such bats tend to avoid very cluttered understoreys where reception of ultrasound signals for spatial orientation and in search of food are more challenging (Kalko and Schnitzler 1998; Schnitzler and Kalko 2001; Rainho et al. 2010). We argue that these seasonal differences in patch use also reflect the changing availability of food and water throughout the year. In the wet season resources are widely available, such that bats can choose those patches with lower levels of understorey clutter, whereas in the dry season resources are more limited and this may drive bats to forage in more cluttered patches as those are also the patches with greater resource availability.

The link between bat distributions and resource availability as a driver of the importance of patch-level variables is further supported by the importance of basal area, canopy cover, vegetation clutter, and tree height in explaining differences in community weighted mean values between forest patches. Both canopy cover and tree height had positive effects on animalivorous bats and negative effects on phytophagous bats, as we had already predicted. Our results show that animalivorous species need higher forest cover in the Savannas of Amapá, as well as forest patches with taller trees. Animalivorous species (e.g., *L. silvicola* and *G. crenulatum*) are more forest-dependent, include top predators, have more fragile populations and are potentially more vulnerable to the loss of forest habitats (e.g., Meyer and Kalko 2008; Martins et al. 2017; Farneda et al. 2018; Carvalho et al. 2021). Phytophagous bats (e.g., *A. obscurus* and *U. bilobatum*) showed an opposite result to animalivorous bats. As phytophagous bats, especially frugivorous species, tend to forage in more open environments such as clearings and forest edges, areas where fruit availability is usually higher, particularly of fruits of pioneer species, they tend to be negatively affected by forest cover and canopy cover (Meyer et al. 2016). Negative effects of vegetation clutter in the wet and dry seasons on CWM of body mass shows that this predictor is an important environmental filter for this functional trait and not just for bat diversity. We would suggest that this pattern may reflect the higher energy costs associated with

flying through more densely vegetated areas that are not compensated by food intake (Norberg and Rayner 1987; Caras and Korine 2009). Similarly, the decreased CWM of wing aspect with increasing canopy cover in the dry season could reflect a restriction of species with a smaller wing aspect (for which the energetic costs of flight are higher - Norberg and Rayner 1987) to patches with greater canopy cover, where the understorey tends to be more open and thus flight is less energetically demanding. However, all these patterns need to be confirmed with physiological studies to assess energy expenditure according to these functional traits.

Taken together, our results suggest that on the one hand, in response to changes in the spatial distribution of resource (e.g., fruits and insects) availability between forest patches throughout the year, bats tend to use the whole landscape in the wet season. On the other hand, there is a reduction in the general abundance and diversity of bats in the dry season, concentrating the abundance in the patches with taller trees, closer to permanent water bodies. In our case, the different species (e.g., *Micronycteris megalotis* and *G. crenulatum*) and lineages (e.g., species of Phyllostominae and Micronycterinae) of bats may also be searching for resources in the continuous *terra firme* and *várzea* (flooded) forests adjacent to the Savannas of Amapá. This movement of bats (or seasonal population fluctuation) in the landscape has already been documented in different studies conducted in Neotropical forests, where bats tend to select habitats that have higher availability of food resources (see Bianconi et al. 2006; Bobrowiec et al. 2014; Ortêncio-Filho et al. 2014). However, this needs to be further investigated and confirmed for Amazonian Savannas and adjacent habitats with the use, for example, of radio tracking or isotope analyses.

Given all of this, processes that impede or limit such seasonal movements, such as the large-scale conversion to soybean and eucalyptus plantations seen in recent years (Barbosa et al. 2007; Carvalho et al. 2019a) could further accelerate the loss of species, functions and lineages where forest cover is naturally lower, as bats use the savanna matrix to move between forest patches (Bernard and Fenton 2007; Carvalho et al. 2021). Indeed, the increase in human activities (mainly commercial plantations, such as soybeans and corn) around forest patches in the Savannas of Amapá has already been shown to

negatively influence the taxonomic and functional diversity of birds (Pandilha et al. 2021). Therefore, conservation measures should also aim to protect the integrity of the savanna matrix, guaranteeing functional connectivity (e.g., Uezo et al. 2005) between forest patches. This will also be important for the maintenance of the ecosystem services that Phyllostomid bats provide, such as seed dispersal and insect population control (Kunz et al. 2011). As such, there is an urgent need to better study these seasonal patterns of landscape use in order to better understand the potential implications of the ongoing substitution of savanna habitat with commercial plantations across the Amazonian Savannas (Barbosa et al. 2007; Carvalho and Mustin 2017; Carvalho et al. 2019a). In addition, disturbances within the forest patches, caused by the increased intensity of the use of savannas as pastures for domesticated cattle and selective logging (e.g., Hordijk et al. 2019), represents a further threat to the bat fauna. Cutting larger trees leads to increased understory obstruction, as it promotes the opening of clearings, and thus the growth of pioneer species (Gauí et al. 2019), which may favor the higher occurrence of more generalist species of bats (Meyer et al. 2016; Rocha et al. 2017; Farneda et al. 2018; Carvalho et al. 2021). A better understanding of these processes would also allow for better landscape-level planning of conservation strategies that can help to protect the fundamental processes, such as seasonal movement, that help to maintain bat diversity throughout the Savannas of Amapá.

Taken together, our results show the importance of considering spatio-temporal patterns of different components of biodiversity in the same study, as responses of species or functional groups do not necessarily follow the same patterns as overall taxonomic, functional and phylogenetic diversity. This is particularly important from a conservation perspective, where such an approach can show the importance of different conservation actions aimed at protecting landscapes, habitats, species and ecosystem processes. Our multi-dimensional assemblage-level and species-specific analyses showed that both proportional forest cover in the landscape and patch-level variables are important for the maintenance of different components of Phyllostomid bat diversity in an Amazonian Savanna landscape. This in turn suggests that conservation plans should consider forest conservation and restoration at the landscape level,

protection of the savanna matrix against ongoing substitution with commercial plantations, and maintenance and restoration of forest patch quality. We also showed that there is seasonal variation in relationships between components of bat diversity and different drivers, strongly suggesting seasonal movements of bat assemblages between different components of this complex landscape. It is therefore crucial to consider these seasonal spatial patterns, and the environmental drivers that shape them, in conservation management plans. In doing so, conservation actions can be implemented that will help to guarantee that Phyllostomid bat species have the necessary resources throughout the year for survival and reproduction, and thus the effective conservation of the bat community and the ecosystem services they provide. In conclusion, our results have direct implications for the elaboration and implementation of conservation strategies in the Amazonian Savannas and, consequently, for bat conservation in the Amazon.

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Author contributions WDC originally formulated the idea. WDC, BSX, IJC, TMM, and KM conducted fieldwork. WDC, LMR and RH performed statistical analyses. WDC, LMR, BSX, RH and KM wrote the drafts of the main manuscript and the online resources. JJT, MVV and JMP reviewed the final version of the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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