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Original Article

Diet of frugivorous bats (Chiroptera: Phyllostomidae) in an ecotonal Cerrado-Atlantic Forest preservation area in southeastern Brazil

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Abstract: Understanding the dietary ecology of frugivorous bats is essential for comprehending their trophic roles and resource use patterns in tropical ecosystems. In this study, we investigated the diet of seven frugivorous bat species of the family Phyllostomidae in the Quedas do Rio Bonito Ecological Park, a Cerrado-Atlantic Forest ecotonal area in southeastern Brazil. We analyzed niche breadth, niche overlap, and seasonal diet variation using both plant-based and bat-based matrices. Data were collected over eight months (December 2019 to September 2020), totaling 40 field days. We captured 256 bats belonging to 14 species from three families (Phyllostomidae, Vespertilionidae, and Molossidae), of which 151 captures were of eight species of Phyllostomidae (six frugivorous and two nectarivorous), and we collected 130 fecal samples, of which 79 contained seeds from seven plant families, with Piperaceae (14.9%), Solanaceae (10.6%), Hypericaceae (5.8%), and Urticaceae (4.3%) being the most representative. The most abundant bat species were *Carollia perspicillata* (n = 66), *Sturnira lilium* (n = 36), and *Glossophaga soricina* (n = 14). *Carollia perspicillata* exhibited the highest niche breadth (B_i = 6.93), followed by *S. lilium* (B_i = 5.71) and *G. soricina* (B_i = 3.00). The observed community-level niche overlap (O_{ik} = 0.53) was not significantly different from random expectations (RA3 null model, p = 0.11), suggesting that the bat assemblage does not exhibit strong dietary structuring. PERMANOVA revealed no significant seasonal differences at the community level, whether analyzed using plant-based (F = 0.69, R^2 = 0.04, p = 0.38) or bat-based matrices (F = 1.57, R^2 = 0.14, p = 0.13), and PERMDISP2 confirmed homogeneity of dispersions between seasons (p = 0.72 and p = 0.91, respectively). However, species-specific analysis for *C. perspicillata* revealed a significant seasonal difference (X^2 = 17.57; p = 0.01), driven by replacement between *Piper aduncum* (rainy season) and *Piper umbellatum* (dry season). For *S. lilium*, no significant seasonal difference was detected (p = 0.29). Our results indicate a predominance of pioneer plants and seasonal resource switching by the most abundant species, highlighting the dietary flexibility of *C. perspicillata* in response to seasonal fruit availability.

Keywords: Bat-plant interactions; Frugivory; Lavras; Parque Quedas do Rio Bonito; Trophic ecology.

Resumo: (Dieta de morcegos frugívoros (Chiroptera:Phyllostomidae) em uma área de preservação ecotonal de Cerrado-Mata Atlântica no sudeste do Brasil). Compreender a ecologia alimentar de morcegos frugívoros é essencial para conhecer seus papéis tróficos e padrões de uso de recursos em ecossistemas tropicais. Neste estudo, investigamos a dieta de sete espécies de morcegos frugívoros da família Phyllostomidae no Parque Ecológico Quedas do Rio Bonito, uma área ecotonal de Cerrado-Mata Atlântica no sudeste do Brasil. Analisamos a amplitude de nicho, a sobreposição de nicho e a variação sazonal da dieta utilizando matrizes com plantas e com morcegos nas linhas. Os dados foram coletados ao longo de oito meses (dezembro de 2019 a setembro de 2020), totalizando 40 dias de campo. Capturamos

256 morcegos pertencentes a 14 espécies de três famílias (Phyllostomidae, Vespertilionidae e Molossidae), das quais 151 capturas foram de oito espécies de filostomídeos (seis frugívoras e duas nectarívoras), e obtivemos 130 amostras fecais, das quais 79 continham sementes de sete famílias de plantas, sendo Piperaceae (14.9%), Solanaceae (10.6%), Hypericaceae (5.8%) e Urticaceae (4.3%) as mais representativas. As espécies de morcegos mais abundantes foram *Carollia perspicillata* (n = 66), *Sturnira lilium* (n = 36) e *Glossophaga soricina* (n = 14). *Carollia perspicillata* apresentou a maior amplitude de nicho (B_i = 6.93), seguida por *S. lilium* (B_i = 5.71) e *G. soricina* (B_i = 3.00). A sobreposição de nicho observada em nível de comunidade (O_{ik} = 0.53) não foi significativamente diferente das expectativas aleatórias (modelo nulo RA3, p = 0.11), sugerindo que a assembleia de morcegos não apresenta forte estruturação alimentar. A PERMANOVA não detectou diferenças sazonais significativas em nível de comunidade, seja analisada com matriz de plantas (F = 0.69, R^2 = 0.04, p = 0.38) ou com matriz de morcegos (F = 1.57, R^2 = 0.14, p = 0.13), e o PERMDISP2 confirmou a homogeneidade das dispersões entre as estações (p = 0.72 e p = 0.91, respectivamente). No entanto, a análise específica para *C. perspicillata* revelou uma diferença sazonal significativa (X^2 = 17.57; p = 0.01), impulsionada pela substituição entre *Piper aduncum* (estação chuvosa) e *Piper umbellatum* (estação seca). Para *S. lilium*, nenhuma diferença sazonal significativa foi detectada (p = 0.29). Nossos resultados indicam predominância de plantas pioneiras na dieta dos morcegos e substituição sazonal de recursos pela espécie mais abundante, destacando a flexibilidade alimentar de *C. perspicillata* em resposta à disponibilidade sazonal de frutos.

Palavras-chave: Interações morcego-planta; Frugivoria; Lavras; Parque Quedas do Rio Bonito; Ecologia trófica.

Introduction

Bats are key components of Neotropical ecosystems, contributing to multiple ecological processes such as seed dispersal, pollination, and arthropod suppression (Muñoz-Lazo et al., 2019; Ramírez-Fráncel et al., 2022). Their interactions with plants have been extensively investigated over recent decades, with particular emphasis on frugivory and its consequences for forest dynamics (Lobova et al., 2009; Jacomassa & Pizo, 2010; Bredt et al., 2012; Sánchez & Giannini, 2018). Frugivorous bats are among the most important consumers of fruits in the Neotropics, and understanding their dietary ecology, including resource selection, niche partitioning, and seasonal variation is essential for comprehending how these animals use available resources and influence plant communities (Fleming & Sosa, 1994; Muscarella & Fleming, 2007). Bats consume fruits from different successional stages (Giannini & Kalko, 2004; Rojas et al., 2012) and a wide range of fruit sizes and structures (Muscarella & Fleming, 2007; Seltzer et al., 2013), reflecting their ecological flexibility. By removing fruits and transporting seeds away from parental plants, bats contribute to dispersion and, consequently, the regeneration of degraded habitats (Jordano et al., 2006; Jacomassa & Pizo, 2010; Ramírez-Fráncel et al., 2022).

Bat-plant interactions have been fundamental to drive the morphological and ecological diversification of the Phyllostomidae, the most diverse bat family in the Neotropics, with approximately half of its species being frugivorous (Torres et al., 2018; Ramírez-Fráncel et al., 2022; Stevens, 2022b). Well-known associations between bat genera and specific plant genera, such as *Artibeus* with *Ficus*, *Carollia* with *Piper*, and *Sturnira* with *Solanum*, illustrate the tight ecological links that have shaped the evolution of both groups (Mello et al., 2004; Brito et al., 2010; Andrade et al., 2013; Martins et al., 2014; Laurindo et al., 2018; Torres et al., 2018). These interactions are not restricted to a single successional stage, bats consume fruits from early-successional species such as *Cecropia* and *Piper*, as well as from mid-to late-successional plants, contributing to forest dynamics at multiple scales (Giannini & Kalko, 2004; Muscarella & Fleming, 2007). In Brazil, frugivorous bats are known to interact with approximately 550 zoochorous plant species from more than 60 families (Lobova et al., 2009; Bredt et al., 2012). The actual number is likely higher, as more recent records from less-sampled regions have not yet been included in comprehensive updates. However, many of these records come from well-studied regions, and there remain significant gaps in our knowledge of bat-fruit interactions in ecotonal and less sampled areas, such as the Cerrado-Atlantic Forest transition zone in southeastern Brazil.

The factors driving dietary specialization observed in some bat genera are still debated (Parolin et al., 2016). Historical, climatic, and anthropogenic factors have been proposed as key drivers (Giannini & Kalko, 2004; Pellón et al., 2021; Sánchez & Giannini, 2018; Stevens, 2022b). In seasonal and anthropized environments, where fruit availability may be restricted to a few species, bat diets can shift in response to resource scarcity (Mello et al., 2004; Genelhú et al., 2023). Stevens (2022b) identified two environmental characteristics that can influence diet: anthropogenic land use leading to habitat fragmentation, and marked annual seasonality. In fragmented landscapes, the reduction in native vegetation complexity may favor species with greater dietary flexibility (Galindo-González, 2004), potentially driving niche expansion and the exploration of alternative food sources, rather than simply forcing bats to rely on a narrower set of resources or to travel longer distances between patches (Mello et al., 2004). Similarly, in seasonal environments, the timing of fruit production can vary considerably between dry and rainy seasons, potentially affecting bat diets and foraging behavior (Genelhú et al., 2023). Nevertheless, seasonality does not always result in distinct, non-overlapping diets between the dry and rainy seasons, as some bat species may switch to alternative resources or adjust their foraging strategies to cope with changes in fruit availability (Stevens, 2022a; Genelhú et al., 2023).

In this study, we examined the diet of frugivorous

bats in an ecotonal Cerrado-Atlantic Forest conservation area in southeastern Brazil, a region where bat-fruit interactions remain poorly documented. The study area, the Quedas do Rio Bonito Ecological Park, is one of the few preserved remnants in the region and provides an opportunity to document the bat diets in a transitional environment. Specifically, we aimed to: (i) describe the diet composition of the bat assemblage, identifying the main plant families and species consumed; (ii) quantify niche breadth and overlap among bat species to assess the degree of resource sharing; and (iii) test whether diet composition, niche breadth, and niche overlap differ between dry and rainy seasons, contributing to a better understanding of how seasonal variation influences bat-plant interactions in ecotonal areas.

Material and Methods

Study Area

The study was conducted at the Quedas do Rio Bonito Ecological Park (QRBEP), a private property of 235 hectares located on the Serra do Carrapato (Fig. 1), in the municipality of Lavras, southern Minas Gerais state (21° 19'S, 44° 59'W). This site is important since it is one of the few preserved areas in the Lavras region, and the park offers both scientific and educational activities. Although classified within the Atlantic Forest domain, this region also presents Cerrado typical vegetation, which characterize it as an ecotone region (Oliveira-Filho & Fluminhan-Filho, 2007). According to the Köppen climate classification system, the climate of the region is classified as Cw, which corresponds to a temperate climate with dry winters and rainy summers (Alvares et al., 2013).

Data Collection

Data collection consisted of eight monthly sampling campaigns, each lasting five days, totaling 40 days in the field. Four campaigns were conducted during the rainy season (December 2019, January, February, and March 2020) and four during the dry season (June, July, August, and September 2020), with sampling effort evenly distributed between seasons (four campaigns per season, each lasting five days). Bats were captured using six mist nets (12 × 2.5 m, 30 m² each) set at ground level (understory), opened at sunset, and closed after six hours, totaling 40 sampling nights. Sampling effort was 1,440 mist-net-hours or 43,200 hm² (following Straube & Bianconi, 2002). Captured individuals were removed from the nets at 30 min intervals and kept in individual cotton bags for 30 minutes to collect fecal samples.

Bats were identified in the field using the identification key of Díaz et al., (2016) and released at the capture site. Fecal samples were stored in 2.0-ml microtubes containing 70% alcohol and labeled with the animal field number. Seeds were analyzed in the laboratory using a stereoscopic microscope. The material was separated into distinct categories. Specific plant seeds were identified to the lowest taxonomic level possible using available literature (Lobova et al., 2009; Lorenzi, 2009; Bredt et al., 2012; Kuhlmann & Fagg, 2018; Lima et al., 2016). Whenever morphological traits (e.g., size, shape, color, and surface texture) allowed unambiguous identification, seeds were identified to species; otherwise, they were assigned to the lowest reliable taxonomic level, usually genus. For all analyses, each identified taxon was treated as a distinct interaction item at the taxonomic level to which it was identified. For items that could not be taxonomically identified, broader categories were used: 'Pulp' for undifferentiated fruit fragments, 'Leaf' for any consumed leaf material, and 'Insect' for all insect remains. It is important to note that mist nets were set exclusively in the understory, which may bias captures toward understory-foraging bats (e.g., *Carollia* and *Sturnira*) and their commonly consumed plants (e.g., *Piper* and *Solanum*), while underrepresenting species that frequently forage in higher strata, such as some *Artibeus* (Rex et al., 2011). However, the use of vertical space by phyllostomid bats is not strictly categorical, and larger *Artibeus* species, for instance, are known to be flexible in their use of vertical space (Rex et al., 2011; Gregorin et al., 2017).

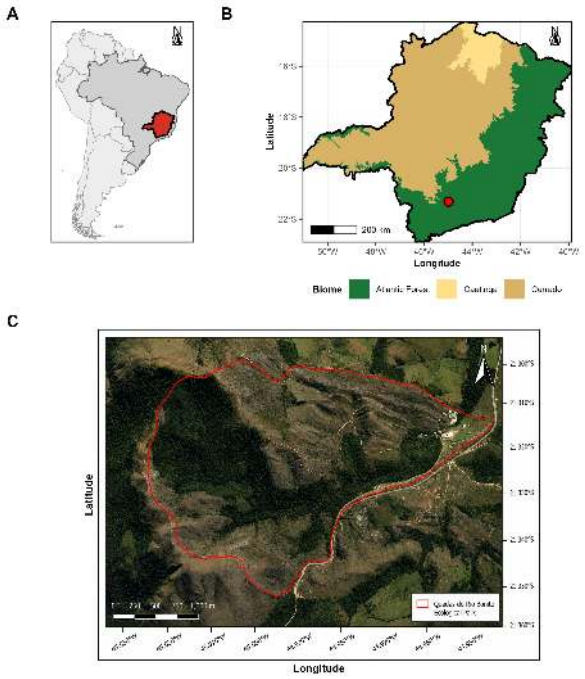

Figure 1: Location of the study site in the municipality of Lavras, state of Minas Gerais, Brazil. (A) South America with Brazil and Minas Gerais highlighted in red; (B) Minas Gerais state showing biomes (Cerrado, Atlantic Forest, Caatinga) and the location of Quedas do Rio Bonito Ecological Park (QRBEP; red dot); (C) Satellite image of QRBEP with the park boundaries (red polygon) and the surrounding landscape. Satellite image source: Google Earth (Image © 2026 Maxar Technologies, © 2026 CNES/Airbus, Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO).

For quantitative analyses (niche breadth, niche overlap, null models, and PERMANOVA), we excluded the categories 'Pulp' and 'Leaf' because they were not iden-

tified to specific plant taxa and could represent multiple resources. These categories were retained at the appendix and in descriptive results as ecologically relevant information, but were not included in the calculation of resource use matrices. Botanical nomenclature followed the Missouri Botanical Garden as stated on the "Tropicos" website (*Tropicos.org*, 2021).

All subsequent analyses were performed at the lowest possible taxonomic level (species whenever identifiable, e.g., *Piper aduncum*, *Piper umbellatum*, and *Solanum granuloso-leprosum*; and genus when necessary, e.g., *Ficus* sp., *Miconia* sp., and *Psidium* sp.; see the appendix). Samples were analyzed to quantify the frequency of occurrence of each food item in the diet of each bat species. Food items were recorded as the number of times each item was present in the samples of each bat species (Mello et al., 2004).

Data Analysis

Sampling completeness was assessed using the Chao1 incidence estimator (Chao, 1984) based on the frequency of unique bat-plant interactions recorded in fecal samples. Completeness was calculated as S_obs/S_est × 100, where S_obs is the number of observed interactions, and S_est is the estimated number of interactions. This analysis was performed for the entire dataset and separately for each season (rainy and dry).

Niche breadth (B_i) for all seven bat species was evaluated using the standardized Levins *index* (Hurlbert, 1978):

$$B_i = \frac{1}{\sum_{j=1}^{r}(P_{ij})^2}$$

where B_i represents the standardized Levins index, and P_{ij} is the proportion of food resource *i* in the total resources used by species *j*. This index ranges from 1 (extreme specialization, single resource used) to the number of resource categories (maximum generalization) (Hurlbert, 1978).

Niche overlap among all bat species was calculated using the Pianka index (O_ik; Pianka, 1973),

$$O_{ik} = \frac{\sum_{j=1}^{r} P_{ij}P_{kj}}{\sqrt{(\sum_{j=1}^{r} P_{ij})^2(\sum_{j=1}^{r} P_{kj})^2}}$$

where O_{ik} is the measure of Pianka's food overlap between species *i* and *k*, P_{ij} is the proportion of food resource *i* in the total resources used by species *j*, and P_{ki}: is the proportion of food item *i* in the total number of items used by species *k*. This index ranged from 0 (no overlap) to 1 (total overlap). These analyses included all seven species, regardless of sample size.

To assess whether the observed niche overlap values differed from random expectations, we used null models with the RA3 randomization algorithm (Gotelli & Entsminger, 2009). RA3 preserves zeros in the original matrix and retains the observed niche breadth of each species while randomizing the identity of consumed items. We performed 5,000 simulations of food category frequencies using the 'EcoSimR' package (Gotelli et al., 2015). A statistically significant deviation was inferred if the observed Pianka index fell outside the 95% confidence interval of the simulated distribution ($p < 0.05$, two-tailed test). This procedure was applied to: (i) all species combined (mean overlap across all pairwise species combinations), and (ii) each species pair individually (*C. perspicillata* vs. *S. lilium*, *C. perspicillata* vs. *G. soricina*, and *G. soricina* vs. *S. lilium*). The overall community overlap was calculated as the mean Pianka index across all pairwise species combinations (excluding pairs with insufficient data).

Seasonal variations in dietary composition at the community level were evaluated using Permutational Multivariate Analysis of Variance (PERMANOVA; 9,999 permutations) implemented in the vegan package (Oksanen et al., 2020). To account for differences in sampling effort and resource dominance, count data were Hellinger-transformed prior to calculating Euclidean distance matrices (Legendre & Gallagher, 2001). To account for non-independence, permutations were block-restricted by plant species for the plant-based matrix and by bat species for the bat-based matrix.

To capture distinct ecological dimensions, PERMANOVA was conducted using two complementary approaches. The first approach used a plant-based matrix, in which plant taxa were arranged as rows and seasons as columns, to evaluate whether the composition of seeds changed between seasons, thereby testing whether the plant community dispersed by bats differed between the rainy and dry seasons. The second approach used a bat-based matrix, in which bat species were arranged as rows and seasons as columns, to evaluate whether bat species shifted their overall resource composition between seasons, thereby testing whether the dietary composition of the bat assemblage differed between seasons when considering each species individually. Homogeneity of multivariate dispersions between seasons was tested prior to PERMANOVA using PERMDISP2 (Anderson et al., 2006). Dietary composition patterns and seasonal centroids were visualized using Principal Coordinates Analysis (PCoA) based on Hellinger distance matrices.

Species-specific seasonal shifts in diet composition were evaluated for *C. perspicillata* and *S. lilium* (species with $\geq$ 10 samples per season) using Chi-square tests of homogeneity. All analyses were conducted in R environment v.4.3.2 (R Development Core Team, 2023) using the 'vegan' (Oksanen et al., 2020), and 'spaa' (Zhang, 2016) packages, and 'ggplot2' (Wickham, 2016), 'dplyr' (Wickham et al., 2023), 'tidyr' (Wickham & Girlich, 2023), 'ggrepel' (Slowikowski, 2021), 'RColorBrewer' (Neuwirth, 2022), and 'patchwork' (Pedersen, 2020) for data manipulation and visualization.

Results

We recorded 256 captures belonging to 14 bat species from three families: Phyllostomidae, Vespertilionidae, and Molossidae. Of these, 151 captures were of eight phyllostomid species, comprising six frugivorous and two nectarivorous species, with 75 individuals captured in the rainy season and 76 in the dry season. The assemblage was strongly dominated by *Carollia perspicillata* (n = 66), followed by *Sturnira lilium* (n = 36), *Artibeus fimbriatus* (n = 20), and *Glossophaga soricina* (n = 14). The remaining species, *Anoura caudifer* (6), *Artibeus lituratus* (2), *Carollia brevicauda* (6), and *Platyrrhinus bilabiatum* (1), were recorded at low abundance. The sampling completeness (Chao1) reached 69.0% overall, being 64.0% in the rainy season and 90.0% in the dry season.

We obtained 130 fecal samples from frugivorous bats, of which 79 contained seeds (60.8%), 115 contained fruit pulp (88.5%), eight contained leaf fragments (6.2%), and six contained insect remains (4.6%) (Appendix). The identified seeds belonged to seven plant families: Piperaceae (14.9%), Solanaceae (10.6%), Hypericaceae (5.8%), Urticaceae (4.3%), Moraceae (1.4%), Myrtaceae (0.5%), and Melastomataceae (0.5%). The predominant plant genera were *Piper, Solanum, Cecropia, Vismia*, and *Ficus*. Folivory was recorded predominantly in *C. perspicillata* (seven records: five rainy, two dry) and once in *S. lilium* (dry season). *Carollia perspicillata* exhibited the highest dietary richness (ten food categories), feeding primarily on fruit pulp, *Piper* spp. (20% of identified seeds), *Vismia* spp. (9.6%), and *Cecropia* spp. (6.4%). *Sturnira lilium* consumed eight food categories, dominated by fruit pulp and *Solanum* spp. (30.4% of identified seeds).

Overall dietary niche breadth (B_i) was highest for *C. perspicillata* (B_i = 6.93), followed by *S. lilium* (B_i = 5.71) and *G. soricina* (B_i = 3.00). Seasonal niche breadth for *C. perspicillata* expanded from the rainy (B_i = 2.64) to the dry season (B_i = 4.76), whereas *S. lilium* maintained relatively stable seasonal values (rainy B_i = 3.00; dry B_i = 3.38) (Figure 2). The mean niche overlap at the community level was O_{ik} = 0.53. Pairwise overlap was highest between *C. perspicillata* and *C. brevicauda* (O_{ik} = 0.71), followed by *G. soricina* and *C. brevicauda* (O_{ik} = 0.58), *G. soricina* and *S. lilium* (O_{ik} = 0.55), and *C. perspicillata* and *S. lilium* (O_{ik} = 0.38).

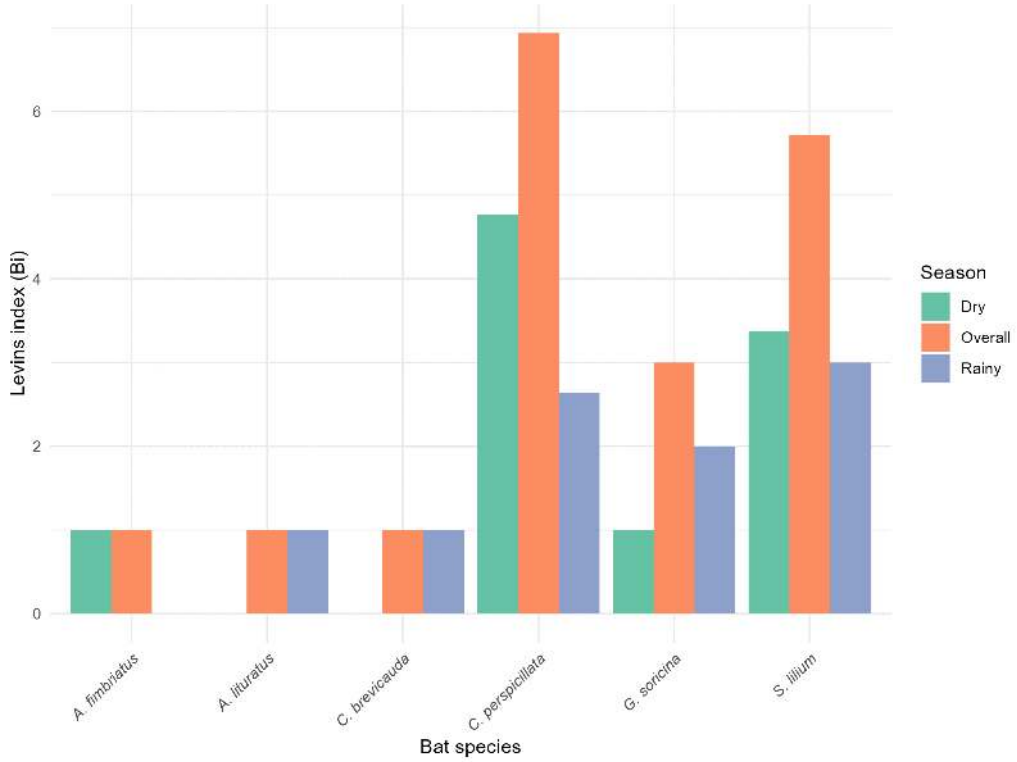

Figure 2: Standardized niche breadth (Levins index) for six bat species in Quedas do Rio Bonito Ecological Park. Values are shown for the overall period (all samples combined), the rainy season, and the dry season.

Null model analysis revealed that the observed community-level overlap did not significantly differ from random expectations (RA3 model, 5,000 simulations: mean simulated = 0.38, 95% CI = 0.18–0.64, upper-tail p = 0.11; Figure 3). This result indicates that dietary overlap among bat species was no greater than expected by chance, suggesting that competition is not a primary driver of resource partitioning in this assemblage. Similarly, none of the focal pairwise comparisons deviated significantly from null expectations (*C. perspicillata* vs. *S. lilium*: p = 0.31, *C. perspicillata* vs. *G. soricina*: p = 0.08, *G. soricina* vs. *S. lilium*: p = 0.08), indicating an absence of competitive structuring.

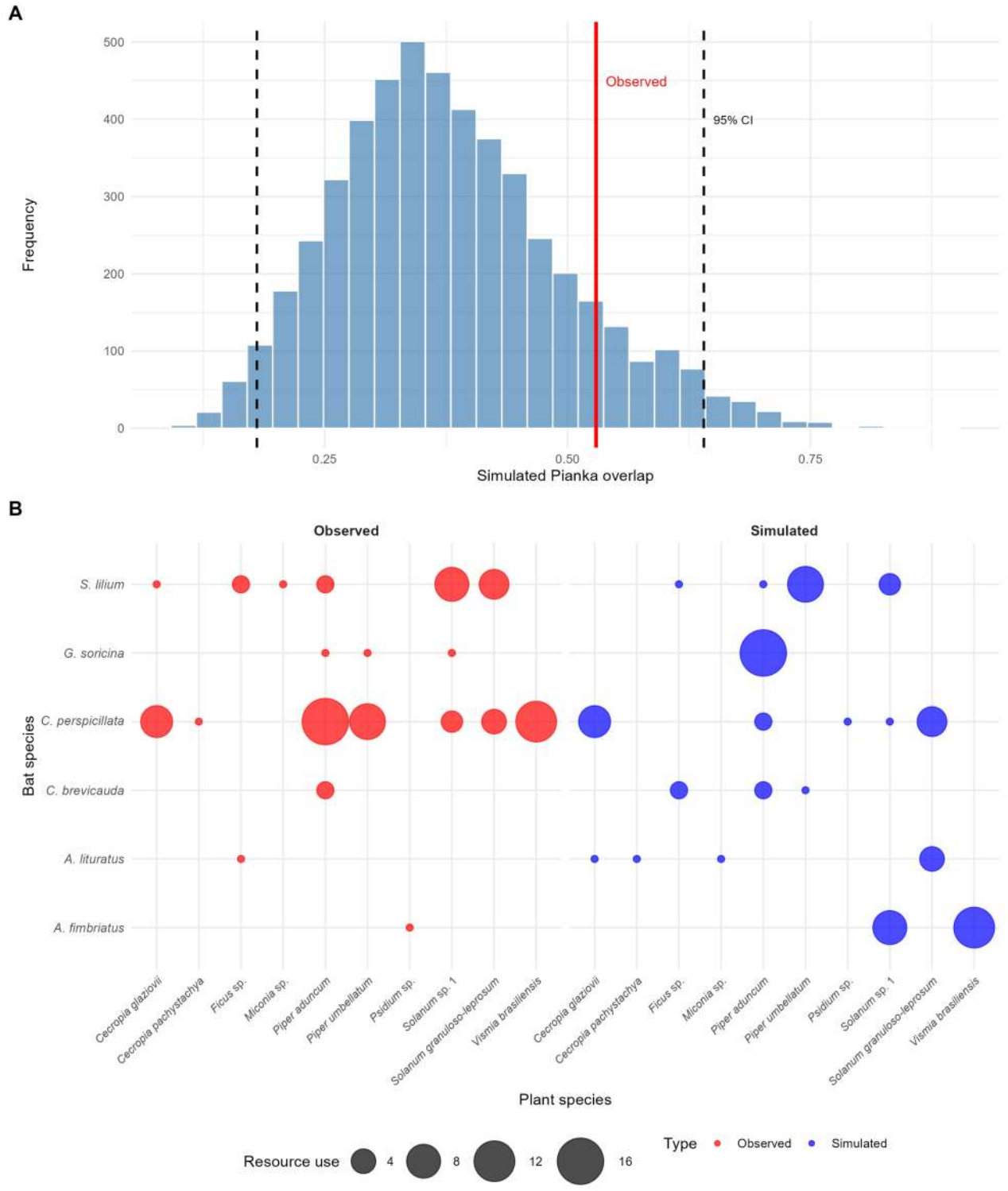

Figure 3: Null model analysis (RA3 algorithm, 5,000 simulations) for community-level niche overlap. (A) Histogram of simulated Pianka overlap values, with the observed index (red vertical line) and 95% confidence intervals (dashed black lines). (B) Bubble plots showing resource use matrices for observed data (red circles) and one randomly simulated null matrix (blue circles). The x-axis represents plant species, and the y-axis represents bat species. The circle area is proportional to resource use.

PERMANOVA based on Hellinger distances indicated no significant seasonal variation in resource composition at the community level. From the plant perspective (plant-based matrix), seasonal diet composition did not differ between the rainy and dry periods ($F = 0.69$, $R^2 = 0.04$, $p = 0.38$; PERMDISP2: $p = 0.72$). From the bat perspective (bat-based matrix), block-restricted permutations across bat species likewise showed no community-wide seasonal shift ($F = 1.57$, $R^2 = 0.14$, $p = 0.125$; PERMDISP2: $p = 0.91$). PCoA ordination scatterplots visually reinforced these results, demonstrating substantial overlap between seasonal centroids across both analytical dimensions (Figure 4).

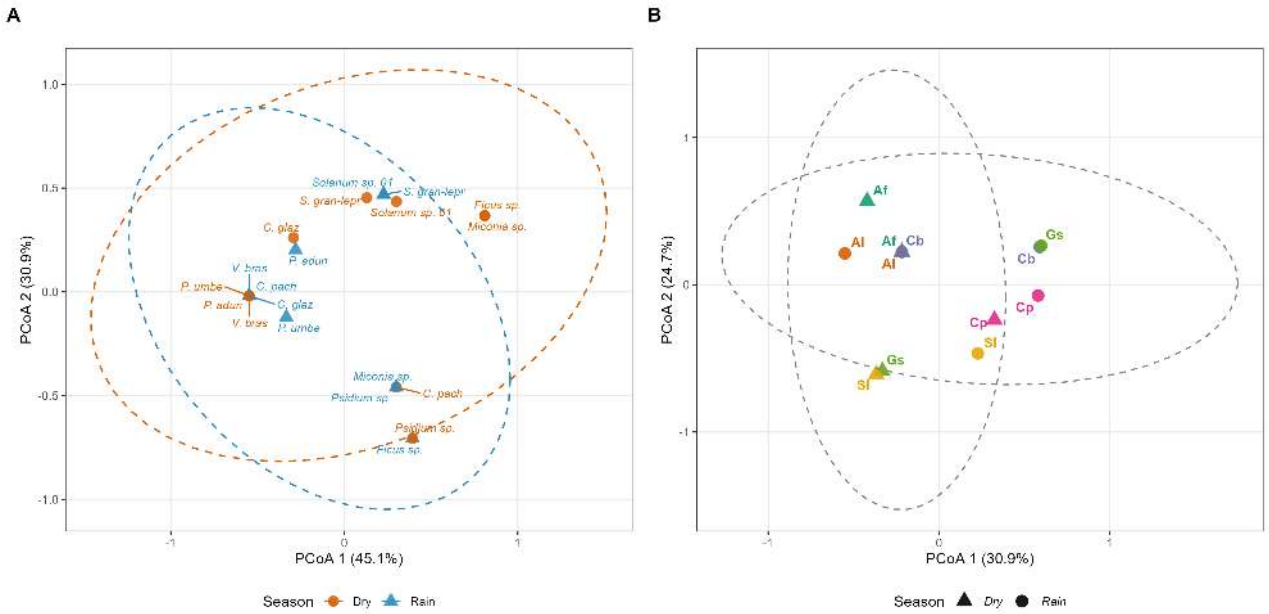

Figure 4: Principal Coordinates Analysis (PCoA) based on Hellinger distance matrices illustrating seasonal variations (dry vs. rainy seasons) in dietary composition at the Quedas do Rio Bonito Ecological Park, southeastern Brazil. (A) Plant-based perspective, showing the ordering of consumed plant taxa across seasons (PCoA 1 = 45.1%, PCoA 2 = 30.9%). (B) Bat-based perspective, showing the ordering of frugivorous bat species centroids across seasons (PCoA 1 = 30.9%, PCoA 2 = 24.7%). Dashed ellipses represent 95% confidence intervals for each season. Plant species abbreviations: C. glaz = *Cecropia glaziovii*, C. pach = *Cecropia pachystachya*, P. adun = *Piper aduncum*, P. umbe = *Piper umbellatum*, S. gran-lepr = *Solanum granuloso-leprosum*, V. bras = *Vismia brasiliensis*. Bat species abbreviations: Af = *Artibeus fimbriatus*, Al = *Artibeus lituratus*, Cb = *Carollia brevicauda*, Cp = *Carollia perspicillata*, Gs = *Glossophaga soricina*, Sl = *Sturnira lilium*.

Carollia perspicillata exhibited a significant seasonal shift in diet composition (X^2 = 17.57, df = 7, p = 0.01), driven by a clear resource replacement between *Piper* species: *Piper aduncum* dominated consumption during the rainy season (14 records), whereas *Piper umbellatum* was predominantly consumed during the dry season (eight records). Conversely, *S. lilium* displayed no significant seasonal shift in diet composition (X^2 = 7.37, df = 6, p = 0.29), maintaining consistent consumption of *Solanum* spp. and fruit pulp across seasons.

Discussion

The most consumed plant families in this study (Piperaceae, Solanaceae, Hypericaceae, and Urticaceae) are pioneers in forest succession and are widely consumed by frugivorous bats (Lobova et al., 2009). This predominance of pioneer plants suggests that the bat assemblage plays an important role in the regeneration of the studied area, a preserved fragment within a disturbed landscape (Saldaña-Vázquez et al., 2013). However, unidentifiable fruit pulp accounted for more than 50% of the feeding records for most species, limiting our ability to fully characterize the diet and potentially obscuring more subtle patterns of resource use. For example, there were unusual records of consumption of insects that may be linked to their high protein content (Orr et al., 2016), suggesting opportunistic foraging behavior to meet nutritional demands. Leaf consumption was also recorded in eight samples, with *C. perspicillata* accounting for seven records and *S. lilium* for one, adding to the limited records of folivory in Neotropical bats (Jorge et al., 2023).

The bat assemblage was dominated by *C. perspicillata* and *S. lilium*, which together accounted for most of the dietary records. This dominance is consistent with other studies in fragmented and disturbed habitats, where these species are often the most abundant frugivores (Aguiar & Marinho-Filho, 2007; Faustino et al., 2021). The most representative plant genera were *Piper, Solanum, Cecropia, Vismia*, and *Ficus*, all of which are typical of early successional stages and provide important resources for frugivorous bats (Lobova et al., 2009). *Carollia-Piper, Sturnira-Solanum*, and *Artibeus-Ficus/Cecropia* associations have been reported across multiple Neotropical biomes (Passos et al., 2003; Aguiar & Marinho-Filho, 2007; Brito et al., 2010; Munin et al., 2012; Andrade et al., 2013; Torres et al., 2018; Laurindo et al., 2018), and our findings are consistent with these patterns. However, the low representation of *Artibeus* in our samples may be partly influenced by understory sampling bias, as some species of this genus are known to forage at higher strata (Aguiar & Marinho-Filho, 2007), although local abundance patterns may also play a role.

Carollia perspicillata consumed *Piper* species (mainly *P. aduncum* and *P. umbellatum*) in 22% of its identified food records. Although this proportion is lower than the values reported in some studies, where *Piper* can constitute over 90% of the diet for some *Carollia* species and for female *C. perspicillata* (Maynard et al., 2019), it

was representative among the identified items. *Carollia perspicillata* also consumed seeds from Solanaceae and Hypericaceae, suggesting dietary flexibility beyond the well-known association with *Piper* (Aguiar & Marinho-Filho, 2007; Torres et al., 2018; Genelhú et al., 2022). This flexibility may be an adaptation to local fruit availability, particularly in ecotonal or disturbed areas where *Piper* may not be the sole abundant resource.

For *S. lilium*, our results showed consumption of *Solanum* species, also aligning with previous studies (Marinho-Filho, 1991; Muller & Reis, 1992; Passos et al., 2003; Brito et al., 2010). However, the frequency of *Solanum* consumption was also relatively low (4 records in the rainy season, 10 in the dry season) compared to unidentified pulp (6 and 20 records, respectively), suggesting that this species may rely more heavily on other resources in this ecotonal area.

Glossophaga soricina, a primarily nectarivorous species, supplemented its diet with fruit. The high proportion of unidentified pulp in its fecal samples (9 records in the rainy season, 2 in the dry season) may be related to its hovering feeding behavior, which could result in the consumption of fruit pulp without the ingestion of seeds (Sazima & Sazima, 2022). Nevertheless, seeds of Piperaceae and Solanaceae found in its feces indicate that seed ingestion and dispersal by defecation do occur, suggesting that even primarily nectarivorous bats can act as seed dispersers for small-seeded plants.

Although no seasonal difference was detected at the community level, when analyzed separately, *C. perspicillata* showed a significant seasonal shift, driven by a seasonal replacement between *Piper aduncum* (predominant in the rainy season) and *P. umbellatum* (predominant in the dry season). This pattern indicates that *C. perspicillata* adjusts its diet to seasonal changes in fruit availability, a strategy that may reduce competition with other frugivores. Such dietary flexibility has been documented for this species in other seasonal environments (Mello et al., 2004; Genelhú et al., 2023) and reinforces its role as a key seed disperser in disturbed and successional habitats. *Carollia* spp. acts as connectors within mutualistic interaction networks, linking multiple modules due to this trophic flexibility (Ligo et al., 2024). No seasonal difference was detected for *S. lilium*, and sample sizes for the remaining species were insufficient for seasonal comparisons. The lack of community-level seasonality may reflect the year-round availability of key pioneer plants, such as *Piper* and *Solanum*, which are known to produce fruits continuously or in multiple pulses throughout the year (Thies & Kalko, 2004), or the similar relative abundances of bat species between seasons (75 captures in the rainy season, 76 in the dry season).

Pairwise null model comparisons revealed that none of the three species pairs tested exhibited niche overlap significantly higher than expected by chance (upper-tail $p > 0.05$ for all pairs). The lack of significant community-level niche structuring, combined with the relatively low mean community overlap, suggests that this bat assemblage is composed of generalist species that share resources without strong competitive exclusion. The abundant pioneer plants (e.g., *Piper* and *Solanum*) likely provide a superabundant and continuous food supply, reducing the need for fine-scale resource partitioning (Faustino et al., 2021). Niche breadth values were highest for *C. perspicillata* and *S. lilium*, indicating that these species are dietary generalists, whereas the remaining species showed low values reflecting their limited dietary records based on identified seeds.

Although this pattern indicates that the bat assemblage is characterized by generalist species with broad diets rather than fine-scale resource partitioning, a finding consistent with studies in other disturbed or ecotonal areas (Faustino et al., 2021; Genelhú et al., 2023). However, the pattern of generalist diets and low niche structuring observed in this study should be interpreted with caution, as several methodological constraints must be considered. First, the high proportion of unidentified fruit pulp (55% of all records) restricts our ability to fully characterize bat diets and may obscure more subtle patterns of resource partitioning. Second, we did not measure resource availability in the environment, which prevents us from making inferences about dietary preference (i.e., selection vs. availability) rather than mere consumption. Third, sample sizes for some species were insufficient for robust seasonal or pairwise analyses. Finally, the low number of captures of canopy frugivores, such as *Artibeus*, is likely a reflection of our understory sampling methodology, which is known to under sample bats that forage in the canopy (Rex et al., 2011; Gregorin et al., 2017). Despite these limitations, our findings provide valuable dietary records from a previously unstudied locality and contribute to the broader understanding of bat-fruit interactions in the Neotropics.

Conclusion

This study provides valuable dietary records for frugivorous bats in the Quedas do Rio Bonito Ecological Park, a Cerrado-Atlantic Forest ecotonal area. The predominance of pioneer plants in the diet and the seasonal resource switching observed for *C. perspicillata* highlight the ecological importance of this species in connecting successional dynamics across seasons. The lack of significant niche structuring (i.e., observed overlap did not differ from random expectations) suggests that interspecific competition is not a major structuring force in this assemblage, likely due to the abundance of pioneer resources. These findings contribute to a broader understanding of bat-fruit interactions in Neotropical ecotonal regions and reinforce the role of frugivorous bats as key components of forest regeneration in human-modified landscapes.

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APPENDIX. Frequency of food items consumed by frugivorous bats of the family Phyllostomidae in the Quedas do Rio Bonito Ecological Park, separated by subfamily and season. R – rainy season; D – dry season. The values represent the number of recorded interactions between bat species and food items (plants or other resources) during each season.

			Family Phyllostomidae													
			Subfamily Carolliinae				Subfamily Glossophaginae				Subfamily Stenodermatinae					
			Carollia brevicauda		*Carollia perspicillata*		*Anoura caudifer*		*Glossophaga soricina*		*Artibeus fimbriatus*		*Artibeus lituratus*		*Sturnira lilium*	
Family	**Species**	Total	R	D	R	D	R	D	R	D	R	D	R	D	R	D
Hypericaceae	*Vismia brasiliensis*	12	0	0	6	6	0	0	0	0	0	0	0	0	0	0
Melastomataceae	*Miconia* sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myrtaceae	*Psidium* sp.	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Moraceae	*Ficus* sp.	3	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Piperaceae	*Piper aduncum*	21	2	0	14	2	0	0	1	0	0	0	0	0	2	0
	Piper umbellatum	10	0	0	1	8	0	0	1	0	0	0	0	0	0	0
Solanaceae	*Solanum granuloso-leprosum*	10	0	0	1	3	0	0	0	0	0	0	0	0	2	4
	Solanum sp.1	12	0	0	1	2	0	0	0	1	0	0	0	0	2	6
Urticaceae	*Cecropia glaziovii*	8	0	0	1	6	0	0	0	0	0	0	0	0	0	1
	Cecropia pachystachya	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Non-identified pulp		115	5	0	35	30	0	1	9	2	3	3	1	0	6	20
Leaf		8	0	0	5	2	0	0	0	0	0	0	0	0	0	1
Insects		6	1	0	1	0	0	0	2	0	2	0	0	0	0	0
Total		208	8	0	66	59	0	1	13	3	5	4	2	0	12	35