Seasonal dietary niche changes in Neotropical bats

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Research Article

Abstract

In the vast Neotropic seasonal environment, the most diverse family of bats, the Phyllostomidae (leaf-nosed bats), includes up to 93 species. As the quality and quantity of food resources fluctuate in the habitats, diet heterogeneity is observed among bat species and regions of the Neotropics. In this study, we investigated by faecal analyses, how the dietary niche (DN) of eight Phyllostomidae bat species (*Artibeus planirostris*, *A. fimbriatus*, *Carollia brevicauda*, *C. perspicillata*, *Chiroderma villosum*, *Glossophaga soricina*, *Platyrrhinus lineatus*, and *Sturnira lilium*) that occur in a karstic area in the Midwest region of Minas Gerais, Brazil, change in response to seasonal food availability. We recorded the consumption of insects and nine plant families. Moraceae was the most frequent, followed by Piperaceae. Given that seasonal dietary changes can be subtle and hardly noticeable along with fluctuating habitat conditions, we performed the DN decomposition of the eight bats species into subniches, by analysing the data with the WitOMI, which is a decomposition of the niche into temporal subniches. By improving the accuracy and details of the results, we assessed the effects of abiotic (precipitation and environmental temperature) and biotic (quantity and quality of food resources) interactions within the phyllostomid bat community. For each species, we compared niche breadth and overlap and found higher values for the dry season among morphologically similar species. The results of our study suggest that ecologically similar bat species coexist occupying different DNs.

Introduction

The ecological niche (EN) concept expresses the relationship of an individual or a population to all aspects of its environment (Hutchinson 1957). Recently, the EN definition was refined and two distinct niche components, Grinnellian and Eltonian, were proposed (Soberón 2007, Stevens 2022a). Environmental conditions and climate heterogeneity determine the Grinnellian niche, whereas the Eltonian niche expresses the local interactions between consumers and resources (Stevens 2022a). EN theory also predicts that similar species will coexist in the same community if they exhibit differences on at least one niche dimension (Chase *et al.* 2002, Geange *et al.* 2011, MacArthur 1958, Ruadreo *et al.* 2019), that is, period of activity (Mancina & Castro-Arellano 2013), use of space (Castaño *et al.* 2018, Pearman *et al.* 2008), or partitioning of food resources (Bolnick *et al.* 2010, Faustino *et al.* 2021, Stephens & Krebs 1986).

The partitioning of food resources, or dietary niches (DNs), plays an important role in decreasing interspecific competition, thus allowing the stable coexistence of functionally similar species at different temporal and spatial scales (Castaño *et al.* 2018, Clare *et al.* 2009, Fleming 1991, García-Estrada *et al.* 2012, Kunz & Parsons 1988, Painter *et al.* 2009). This ecological mechanism is an important determinant in the structuring of the bat community, which in many cases consists of several ecologically and morphologically similar species (i.e. size, mobility, type, and form of foraging) that inhabit the same place (Bolnick *et al.* 2010, Shipley & Twining 2020, Stevens 2022b). Example of this is the Phyllostomidae, most taxonomically diverse bat family both in terms of the number of genera and feeding strategies (Baker *et al.* 2003, Rojas *et al.* 2012). This family stands out in having a wide distribution throughout the Neotropical Region and morphological diversification associated with heterogeneity in resource use among species (Freeman 2000, Stevens 2022b).

For fruit bats, DN partition is strongly influenced by three main factors: 1, the local diversity of plants (Fleming 1993, Lobova *et al.* 2009); 2, the changes caused by the fragmentation of the environment (Faustino *et al.* 2021, Muñoz-Lazo *et al.* 2018, Stevens 2022b); and 3, temporal changes in the availability of these resources (Fleming 1993, Stevens 2022b). The last two factors are probably the most influential in the diet of bats, given that in anthropogenically modified landscapes like the Brazilian Cerrado, plant species that bear fruit for long periods, or that bear
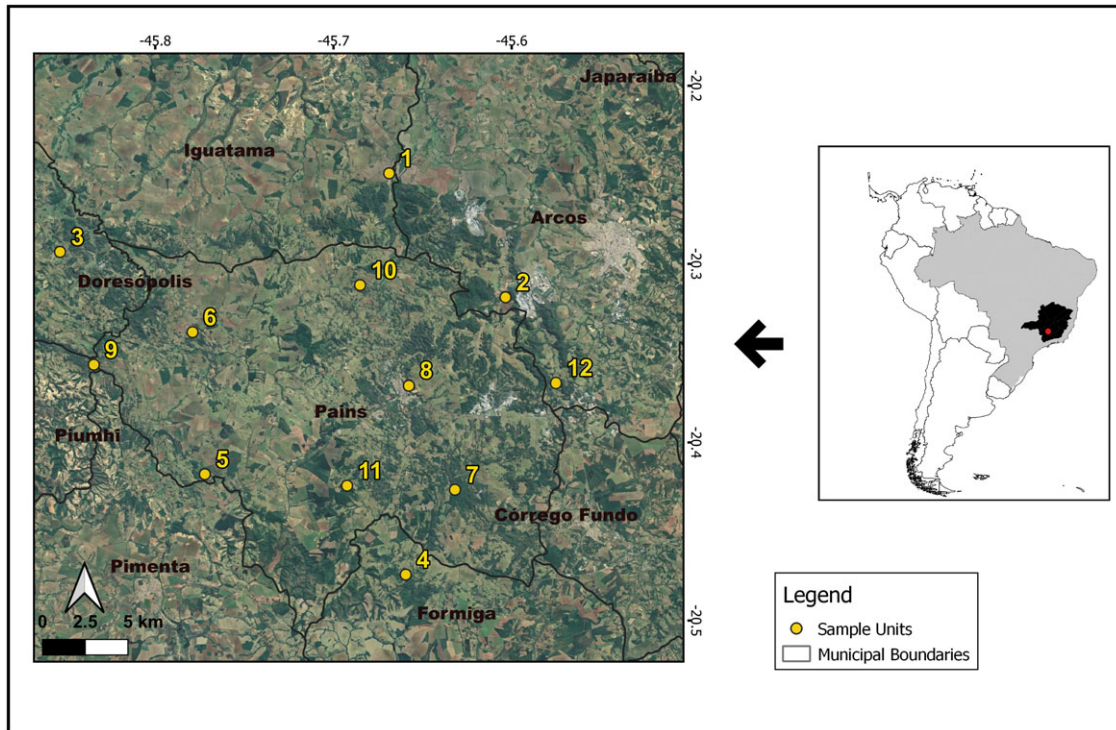
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Figure 1. Map of sample collection points in the Midwest region of the state of Minas Gerais, Brazil.

fruit more than once a year, are the most consumed ones (Heithaus *et al.* 1975, Jacomassa & Pizo 2010, Laurindo *et al.* 2017, Passos & Graciolli 2004, Stevens & Amarilla-Stevens 2021, Stevens 2022b).

Besides important families like Leguminosae, Myrtaceae, Melastomataceae, and Rubiaceae, calcareous rocks known as karsts range through the Cerrado (Pennington *et al.* 2018, Pennington *et al.* 2000). This Biome covers about 24% of the Brazilian territory (Ribeiro & Walter 2008) and more than 57% of the state of Minas Gerais (Machado *et al.* 2004). On areas of fertile soil, which are often associated with calcareous rock, tropical dry forests (TDFs) occur (Dexter *et al.* 2018). These vegetation structures, adapted to the seasonality of the climate, show a leaf flush semideciduous and deciduous regime, resulting in a diversified and singular landscape that must be conserved (Dexter *et al.* 2018). Nevertheless, the agrobusiness, livestock rising, city expansion, and mining activities represent potential drivers to shortening the length of the Brazilian Cerrado (Sano *et al.* 2019).

We carried out a study to know the feeding habits of fruit bats of the Phyllostomidae family, in a karst region located in the midwest portion of Minas Gerais/Brazil, seeking to identify which items are present in their diet, and verifying dietary changes according to seasonal variation and if the coexistence of congeneric species pairs of bats is facilitated by DN differentiation based on seasonal variation. It is expected that with seasonal change, resource abundance will reflect on dietary diversity, with higher amplitude and overlap values during drier periods.

Methods

Study area

The study was carried out in the karst province of Alto São Francisco, also called karst of Arcos, Pains, and Doresópolis

(Figure 1) (Menegasse *et al.* 2002). The region is located in the Cerrado domain, coinciding with the inland limits of the Atlantic Forest. The local native vegetation lies highly uncharacterised as most of it was converted into pastures, crops, and other cultures (e.g. corn, eucalyptus, and coffee) (Oliveira *et al.* 2012, Sano *et al.* 2010). Around calcareous outcrops in the Cerrado, deciduous stationary forest biotype (dry forest) remarkably characterised by the leaf flush deciduous and semideciduous regime is found (Melo *et al.* 2013). This vegetation is known as 'Mata de Pains', in the study area (Barbosa 1961).

The climate of the region, according to the Köppen classification system, is of the Cwa type, that is, a subtropical climate with dry and mild winters and humid and hot summers (Alvares *et al.* 2013). The average annual temperature is around 20°C, with a minimum average of 12°C in the coldest month and an average maximum of 30°C in the hottest month. The average annual rainfall is approximately 1,500 mm (Nimer 1989).

Sampling of Chiroptera fauna and use of food resource

Six field expeditions were conducted for 1 year in February, March, April, May, August, October, and November 2020, and February and April 2021, covering dry and rainy seasons, including 12 sampling sites (outcrops with the presence of caves as the centroid). Sampling sites are far at least 5 km. At each site, one 12×2.5 m mist-net was arranged in the cave entrance blocking it completely or most of it. Five 12×2.5 m mist-nets were arranged at the border of outcrops near the cave entrance. The nets were open for 6 hours from sunset totalling 1,080 m²h for each site and a total of 19,960 m²h for the areas as a whole. Bat identification was based on Díaz *et al.* (2016). All handling procedures followed the recommendation of Sikes *et al.* (2016).

Faecal samples collected during handling of animals in the net, and in the cloth bags, were placed in plastic microtubes containing

70% alcohol, labelled, and then taken to the laboratory for identification under a stereomicroscope. The material was separated into three categories (seeds, insect fragments, and pulp). The seeds were counted and identified to the lowest possible taxonomic level consulting the available bibliography (Bredt *et al.* 2012, Kuhlmann 2018, Lima *et al.* 2016, Lobova *et al.* 2009, Lorenzi 1992, 1998, 2009). The botanical nomenclature followed the Missouri Botanical Garden on the 'Trópicos' website (www. tropicos.org) (Tropicos.org 2021). Insect and pulp fragments were quantified when they were found in samples (Mello *et al.* 2004).

Data analysis

Analyses were carried out only with bat species with 10 or more samples (see Table 1). We initially analysed differences in food consumption by bats between the rainy and dry seasons using PERMANOVA, a Bray–Curtis multivariate permutation analysis of variance with 9,999 random permutations (Anderson *et al.* 2006), followed by a PERMIDISP, to test whether the variation between seasons around its centroid was significantly different from each other (Anderson *et al.* 2006).

To calculate niche overlap among bat species, the Pianka index (Pianka 1973) was used, which ranges from 0 (no overlap) to 1 (total overlap). The observed overlap values were statistically compared to reference ones from null models, in which 5,000 permutations of the frequencies of food categories were performed for the Pianka index (Gotelli *et al.* 2015). Through randomisation of overlap in use of food resources, it is possible to identify whether there is a greater similarity between species of the community exploiting resources (greater overlap observed than expected by chance) or segregation in the use of resources (greater than the expected at random) (Gotelli *et al.* 2015). For these simulations, the randomisation algorithm number 3 (RA3) was used to exchange niche utilisation values between each row of the matrix (Gotelli & Entsminger 2009). This algorithm was pointed out by Winemiller & Pianka (1990) as the one that presents the best statistical properties to detect overlapping patterns of non-random niches (Gotelli & Entsminger 2009).

To evaluate the species DN, we performed an analysis of niche marginality (Outlying Mean Index [OMI]), which is an ordination technique designed to explicitly take into account the niche of each species within a community and determine its marginality (Baldrich *et al.* 2021, Dolédec *et al.* 2000). For each taxonomic unit, the analysis returns three niche parameters: OMI (base of analysis), tolerance (Tol), and residual tolerance (RTol). The marginality (OMI parameter) of a species corresponds to its niche position in an n-dimensional space, where the OMI parameter is defined as the squared Euclidean distance between the average conditions used by a species and the average conditions of the sampled parameters (Baldrich *et al.* 2021, Dolédec *et al.* 2000, Karasiewicz *et al.* 2017). A high marginality value implies that the taxonomic unit is uncommon, or with few occurrences, compared to a low value, which indicates more common and abundant species. (Dolédec *et al.*, 2000; Karasiewicz *et al.*, 2017). For this analysis, we made two matrices: one with the abundance values of the collected bat species separated by sampling units and a second containing the amount of food resources consumed by bat species.

The OMI analysis provides information on niche breadth of species with the tolerance parameter (Tol). High and low tolerance values are associated with taxa that occur in broad ranges (generalists) and limited ranges (specialists) of the conditions (Baldrich *et al.* 2021), respectively. The residual tolerance (RTol)

quantifies the information lost after dimensional reduction (Karasiewicz & Lefebvre 2022). This parameter evaluates the reliability of the variables used to define the species' niche (Dolédec *et al.* 2000, Karasiewicz *et al.* 2017). The statistical significance of the OMI analysis was tested using Monte Carlo permutations by comparing the observed marginality with 10,000 simulated marginalities, which compare the marginality of observed species with the values from the null hypothesis, assuming species with different habits (Baldrich *et al.* 2021, Dolédec *et al.* 2000).

In the next step, we performed a niche decomposition analysis into subniches (within outlying mean indexes [WitOMI]). The decomposition helps to unfold niche dynamics, highlighting the influence of habitat conditions, such as seasonality on the species at a given time and/or space (Karasiewicz *et al.* 2017). The WitOMI indices use the space created by the OMI analysis and integrate new features that allow the division of niches into subniches, linked to temporal subsets. It promotes the comprehension of how community responds to changing environmental conditions at the individual scales (Karasiewicz *et al.* 2017, Saccò *et al.* 2020).

For example, the values of the marginality (OMI) and tolerance (Tol) parameters provided by the OMI may be negatively correlated, and as a result, we can expect that more common species (low marginality) will have broader niches (high tolerance), and uncommon species (high marginality) will have more restricted niches (low tolerance). However, when we perform the decomposition into temporal (seasonal) subniches of these species, this negative correlation may not happen, for example, we can find species with both low WitOMI and Tol values, that is, abundant but with a restricted niche.

For the niche overlap analysis and overlap simulations, 'EcoSimR' package was used (Gotelli *et al.* 2015). For OMI and WitOMI analyses, 'ade4' (Dray & Dufour 2007) and 'subniche' packages (Karasiewicz *et al.* 2017) were used, respectively. For the PERMANOVA and PERMIDISP analyses, 'pairwiseAdonis' (Martínez Arbizu 2020) and 'vegan' (Oksanen 2020) packages were used. All analyses were performed using the R program (R Development Core Team 2021).

Results

Food resource

A total of 499 faecal samples were collected from 15 species of phyllostomid bats. *C. perspicillata* (N = 197) presented seeds belonging to five plant families, *A. planirostris* (N = 146) preferentially consumed fruits of plants from the Moraceae and Myrtaceae families, *G. soricina* (N = 35) consumed mainly Piperaceae, *S. lilium* (N = 31) feed on Cucurbitaceae, and *P. lineatus* (N = 29) showed a predominance of seeds from the Moraceae. Other species of bats had a low number of samples (Table 1).

Total samples analysed, 263 (52.7%) contained seeds, 216 (43.2%) contained pulp remains, and 20 (4.1%) had insect fragments. The seeds found in the faeces are distributed in nine families of plants, being Moraceae (31.5%) the most frequent, followed by Piperaceae (28.5%), Solanaceae (11.4%), and Urticaceae (4.5%) (Table 1). The PERMANOVA analysis showed no difference in food resource between the dry and rainy seasons ($R^2 = 0.01$; F = 0.55; p = 0.59), and homogeneity of dispersions found some difference (rain = 7.786; dry = 9.527), but not significant (F = 0.12; p = 0.73).

Table 1. Occurrence of food items in the diet of bat species of the family Phyllostomidae

Family Phyllostomidae — Subfamily Carolliinae: *Carollia brevicauda*, *Carollia perspicillata*. Subfamily Glossophaginae: *Anoura caudifer*, *Anoura geoffroyi*, *Glossophaga soricina*. Subfamily Phyllostominae: *Phyllostomus discolor*, *Phyllostomus hastatus*. Subfamily Stenodermatinae: *Artibeus fimbriatus*, *Artibeus lituratus*, *Artibeus planirostris*, *Chiroderma doriae*, *Chiroderma villosum*, *Platyrrhinus lineatus*, *Sturnira lilium*, *Vampyressa pusilla*.

Family	Species	C. brevicauda R	C. brevicauda D	C. perspicillata R	C. perspicillata D	A. caudifer R	A. caudifer D	A. geoffroyi R	A. geoffroyi D	G. soricina R	G. soricina D	P. discolor R	P. discolor D	P. hastatus R	P. hastatus D	A. fimbriatus R	A. fimbriatus D	A. lituratus R	A. lituratus D	A. planirostris R	A. planirostris D	C. doriae R	C. doriae D	C. villosum R	C. villosum D	P. lineatus R	P. lineatus D	S. lilium R	S. lilium D	V. pusilla R	V. pusilla D
Cucurbitaceae	*Gurania lobata*	1	0	14	4	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	2	0	0	0	0	0	0	5	1	0	0
Hypericaceae	*Vismia* spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Melastomataceae	*Miconia* spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Myrtaceae	*Psidium* spp.	0	0	0	2	1	1	0	0	0	0	0	0	0	0	1	0	1	0	7	3	0	0	0	0	0	1	0	1	0	0
Moraceae	*Ficus* aff. *gomelleira*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	8	0	0	0	0	0	2	2	0	0	1
	Ficus sp. 1	0	0	2	2	0	0	0	0	0	0	0	1	0	0	1	1	0	1	15	4	1	0	1	5	2	2	0	0	0	0
	Ficus sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	0	1	0	0	0
	Maclura tinctoria	0	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piperaceae	*Piper amalago*	1	0	27	13	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	Piper umbellatum	1	2	2	8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	Piper sp. 1	0	0	3	3	0	0	0	0	5	1	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Rubiaceae	*Cordiera sessilis*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0
Solanaceae	*Solanum americanum*	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
	Solanum paniculatum	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	Solanum sp. 1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Solanum sp. 2	1	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6	2	0	0	0	0	0	0	0	1	0	0
Urticaceae	*Cecropia glaziovii*	0	0	1	5	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	Cecropia pachystachya	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Non-identified pulp		0	4	33	52	1	0	0	1	4	13	0	0	0	0	5	5	0	0	20	37	3	0	1	1	5	10	10	10	0	1
Insects		0	0	1	4	1	0	0	0	2	2	0	2	2	2	0	0	0	0	2	0	0	0	0	1	0	0	1	0	0	0
Total		4	6	96	101	3	1	0	1	18	17	0	4	3	3	12	6	1	1	86	60	4	0	3	7	13	16	17	14	0	2

R = rain; D = dry.

Table 2. Niche overlap values for dry and wet seasons, shown above and below the diagonal, respectively

	Af	Ap	Cb	Cp	Cv	Gs	Pl	Sl
Af		0.96	0.87	0.93	0.37	0.97	0.97	0.95
Ap	0.67		0.86	0.91	0.28	0.95	0.98	0.94
Cb	0.16	0.19		0.90	0.17	0.87	0.85	0.91
Cp	0.71	0.56	0.50		0.21	0.94	0.91	0.95
Cv	0.57	0.65	0	0.45		0.26	0.36	0.18
Gs	0.45	0.43	0.20	0.55	0.47		0.96	0.95
Pl	0.82	0.87	0	0.62	0.66	0.46		0.92
Sl	0.90	0.65	0.26	0.78	0.51	0.49	0.74	

Ap = *A. planirostris*; Af = *A. fimbriatus*; Cb = *C. brevicauda*; Cp = *C. perspicillata*; Cv = *C. villosum*; Gs = *G. soricina*; Pl = *P. lineatus*; Sl = *S. lilium*.

Table 3. Result of OMI and WitOMI analyses

	OMI				WitOMI dry				WitOMI rain			
Species	OMI	Tol	Rtol**	p	WitOMIG	Tol	Rtol	p	WitOMIG	Tol	Rtol	p
A. fimbriatus	3.20	1.67	25.5	**0.05**	8.03	1.80	17.0	**0.05**	3.73	2.17	21.1	0.39
A. planirostris	0.16	1.45	20.2	0.79	0.42	3.62	12.4	0.47	0.13	0.60	22.1	0.68
C. brevicauda	6.82	1.90	14.9	0.08	24.8	0	0	**0.04**	6.54	2.76	12.2	0.62
C. perspicillata	0.07	2.13	18.6	0.80	0.19	3.04	12.3	0.64	0.14	2.62	20.0	0.64
C. villosum	6.18	1.84	20.5	**0.01***	18.8	5.61	10.3	**0.04**	6.71	2.89	11.8	0.50
G. soricina	0.34	2.81	19.6	0.52	0.79	2.10	13.1	0.22	0.25	2.65	21.3	0.58
P. lineatus	1.76	1.43	24.0	**0.05**	4.32	6.61	11.0	**0.04**	2.87	0.72	24.2	0.52
S. lilium	1.51	1.63	16.2	0.17	3.67	6.78	10.6	0.14	3.05	1.52	12.8	0.80
Average marginality	2.50			**0.003**				**0.03**				0.78

OMI = Outlying Mean Index; WitOMIG, marginalities from the average resources condition G; Tol = tolerance; Rtol = residual tolerance and average marginality.
*Bold values are statistically significant.
**Rtol = Residual tolerance represents the variance in the species dietary niche that is not taken into account by the marginality axis.

DN analysis

Niche overlap values were higher between *P. lineatus* × *A. planirostris* (Øjk = 0.96), *A. fimbriatus* × *S. lilium* (Øjk = 0.94), and *A. fimbriatus* × *P. lineatus* (Øjk = 0.92). The smallest overlap found was between *C. villosum* × *C. brevicauda* (Øjk = 0.23) (see Table 1 of the supplementary material). During the analysis of different seasons, it was observed that the overlap values were higher in the dry season compared to the rainy seasons ones (Table 2). The community presented an overlap of 0.72, which is greater the expected by chance (Pobs > Pesp = 0.16, p < 0.01), revealing an overlap in the diet between the species in the area. Divided by season, the dry season showed greater overlap 0.76 (Pobs > Pesp = 0.10, p < 0.01) than rainy season of 0.51608 (Pobs > Pesp = 0.21, p < 0.01) (for more information, see supplementary material).

The first two axes of the OMI accounted for 73.23% of the explained variability (OMI1: 51.39% and OMI2: 21.85%). The mean marginality of the species was significant (p < 0.01), suggesting an influence of food resource (Table 3). Most taxa had low OMI values indicating common use of resources (OMI < 2). *Artibeus planirostris* (p = 0.05), *C. villosum* (p < 0.01), and *P. lineatus* (p = 0.05) presented a well-marked niche for the dry season. *Carollia brevicauda* had the highest marginality value

(OMI = 6.80) followed by *C. villosum* (OMI = 6.10), and *C. perspicillata* and *A. planirostris* with the lowest values (OMI = 0.07 and 0.16, respectively). The high/low values of marginality indicate that the species are uncommon/common, respectively (Dolédec *et al.* 2000). We found higher values of niche breadth (tolerance parameter) for the dry season, these results indicate a niche expansion for this season (Figure 2), *Glossophaga soricina* and *C. perspicillata* had the highest tolerance values (Tol = 2.81 and 2.13), and *P. lineatus* and *A. planirostris* were the lowest (Tol = 1.43 and 1.45).

The marginality values of the seasons presented *C. perspicillata* with the lowest value and *C. brevicauda* with the highest for the dry period; for the rainy period, *A. planirostris* was lowest and *C. villosum* was highest. Regarding the tolerance values, the highest was for *S. lilium* in the dry season and *C. villosum* in the rainy season, and the lowest for the dry season with *C. brevicauda* and rainy with *A. planirostris*. We also found higher values of the tolerance parameter for the dry season, indicating that the niche breadth is greater for this season (Table 3). On subniches (WitOMI)', we found significant values only for the dry season with *A. fimbriatus* (p < 0.05), *C. brevicauda* (p < 0.05), *C. villosum* (p < 0.05), and *P. lineatus* (p < 0.05). Regarding the most influential resources in the realised niches of the bats, *Maclura*
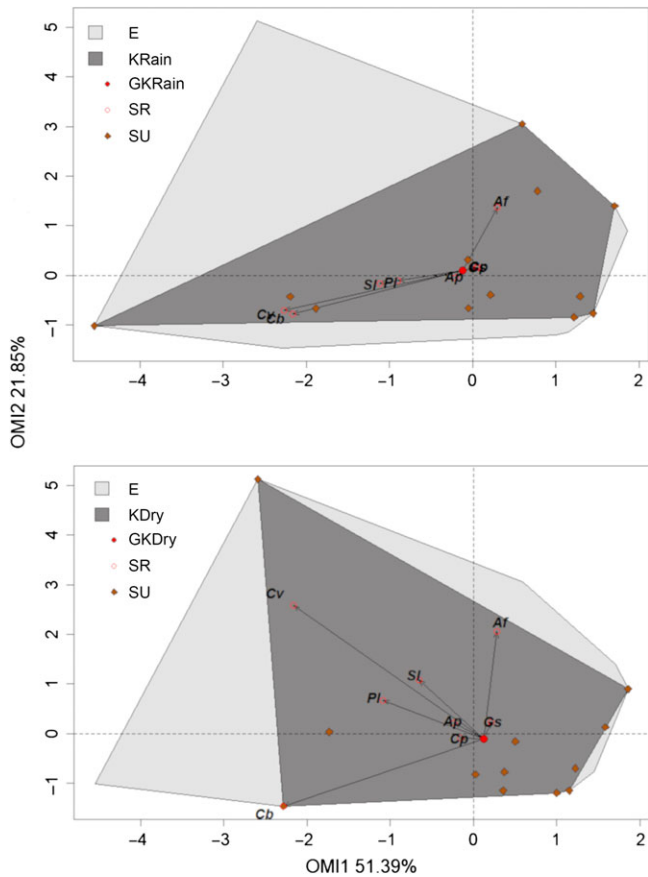
Figure 2. Distribution of bat species within the niche space realised, dry and rainy periods, respectively. For the rainy season, we have an overlap between *C. perspicillata* and *G. soricina*. Arrows represent the marginality of average resource conditions. Marginality measures the distance between the average conditions of the resources used by the species (species centroid) and the average conditions of the resources of the sampled areas (origin of the niche space). E = realised niche space, K = subniche, GK = average condition in each subniche, SR = realised subniche of each species, and SU = sample units. For more details on the niche indices, see Karasiewicz et al. (2017).

tinctoria (p < 0.05) for the dry period and *Gurania lobata* (p < 0.05), *Maclura tinctoria* (p < 0.05), and *Psidium* ssp. (p < 0.05) for the rainy season have contributed more (see supplementary material).

Discussion

Food resource

Our results are consistent with those found in the literature, with the genera *Artibeus*, *Carollia*, *Glossophaga*, and *Sturnira* being more frequent in highly fragmented and anthropic regions and interacting with plants of the Piperaceae, Moraceae, Myrtaceae, Solanaceae, and Urticaceae (Fleming 1993, Lobova et al. 2009, Marinho-Filho 1991, Mello et al. 2004, Mikich 2002, Parolin et al. 2016, Pellón et al. 2021, Stevens 2022b). The fruits of these plants have characteristics that influence selection and consumption, such as accessibility, fruit position outside the foliage, and long stems, which protect the fruit from attacks by flightless animals (Fleming 1993, Muller & Reis 1992). Samples containing only pulp may represent fruits with large seeds, and not ingested, or fruits where the bat ingests the pulp and spits out the seed, or even destroys the seeds (Nogueira & Peracchi 2002).

Although overlap in diet composition was observed among bat species in the dry season, differences in the proportions of items consumed between species reveal a resource-sharing mechanism that allows species to co-occur (Brito et al. 2010). This sharing reflects variation in fruit diet according to the supply of resources in the environment (Passos et al. 2003), but also complemented by insect consumption, for example (Aguiar & Marinho-Filho 2007, Gnocchi et al. 2019, Mello et al. 2004). Consumption of arthropods may be related to their high concentration of proteins (Orr et al. 2016).

Carollia perspicillata was more abundant during our field work, although this is not in agreement with other finds reported in the literature on bat feeding ecology (Faustino et al. 2021, Passos et al. 2003, Pinto & Ortêncio Filho 2006, Silveira et al. 2011). The dominance can be explained by the fact that *C. perspicillata* feeds on fruits of plants which occur in open areas such as forest edges (Reis et al. 2011) and on various strata of vegetation (Faustino et al. 2021, Silveira et al. 2011, Silveira et al. 2020). Futhermore, it takes different shelters and makes its way even through disturbed areas (Muller & Reis 1992), as in the present study. The literature, as well as our study revealed that *Glossophaga soricina* feeded on insects and mainly on Piperaceae (Gnocchi et al. 2019; Martins et al. 2014; Munin et al. 2012). *Sturnira lilium* is specialised for the consumption of *Solanum* (Jacomassa et al. 2021, Mello et al. 2008); but for the area, the largest number of samples was from the Cucurbitaceae family.

Our results on the number of samples per season did not show significant differences, and this is probably related to the lack of seasonality of consumed fruits (Fleming 1986), which led to similar amounts for both seasons, especially due to the two most abundant species, *C. perspicillata* and *A. planirostris*.

DN interactions

Our results indicate that there is a greater increase in niche overlap during the dry season, suggesting that there is potential competition among species, and for them to coexist in equilibrium, or that there must be differentiation in another dimension of the niche, not measured in this study (Lopez & Vaughan 2007, Faustino et al. 2021, Munin et al. 2012). The high overlap during this season probably results from limited resource availability and anthropogenically modified landscapes (Stevens 2022c). In this sense, when resources are limited, niche differentiation plays a key role in species coexistence (Hardin 1960, Johnson & Bronstein 2019), for example, by decreasing niche breadth, mechanisms such as niche partitioning and complementarity facilitate coexistence between sympatric species with similar habitat preferences (MacArthur 1958, Pianka 1976, Shipley & Twining 2020) or show occasional specialisation in a smaller set of preferred resources (Bolnick et al. 2010, Faustino et al. 2021).

This occasional specialisation in a smaller set of resources in seasonal times is important for the species because, in the face of more intense competition, bats restrict the use of a shared resource (Carvalho & Cardoso 2020). This may give them an advantage in exploiting these resources over other generalist species (Carvalho & Cardoso 2020, Muñoz-Lazo et al. 2019). Stevens (2022b), in his study for the Atlantic Forest, warns that food seasonality together with habitat modification is the main driver of reduced specialisation and increased overlap of bat diets. We also expected higher values of niche breadth during the dry season, and our results show a niche expansion (see Figure 2), and this is in line with the optimal foraging theory, where individuals should specialise when

resources are plentiful, but when faced with scarcity they tend to increase the number of items included in the diet (Muñoz-Lazo *et al.* 2019; Stephens & Krebs, 1986).

We also observed *C. perspicillata* and *A. planirostris* with the highest values of niche breadth, indicating that their diet is not concentrated only on a few resources and that they coexist in great abundance (Faustino *et al.* 2021). For *A. planirostris*, we found low tolerance values Tol) in the rainy season and high values in the dry season, which may indicate that this species expands its niche when there is an ecological opportunity (high resource availability) (Carvalho & Cardoso 2020). However, the low marginality values (WitOMI) show that it remains specialised on some number of items, which for our study may be its affinity for plants of the family Moraceae (Laurindo & Vizentin-Bugoni 2020) or a bias created by the number of samples containing only pulp (39% of samples).

For *C. perspicillata*, even confirming its preference for plants of the genus *Piper* (Pellón *et al.* 2015), the low values of marginality, and the number of insect samples in their faeces, show a wide food spectrum with a characteristic close to omnivory (Gnocchi *et al.* 2019). *Platyrrhinus lineatus* and *S. lilium* had the highest tolerance values in the dry season, thus being considered generalists, while in the rainy season they presented low values, thus adopting a punctual specialist profile, as indicated by Faustino *et al.* (2021), a restricted diet does not always indicate specialisation, and the species can be induced to consume a certain temporarily abundant food source.

The analysis showed greater overlap in bat diet than random expectation (Arriaga-Flores *et al.* 2012, Mancina & Castro-Arellano 2013, Sánchez & Giannini 2018, Stevens & Amarilla-Stevens 2021, Stevens 2022c), and two factors that may help to understand this result. First, plant phenological changes that concomitantly lead to seasonal changes in diet, forcing bat species to be more general in their resource utilisation (Stevens 2022c); second, habitat modification, which in turn can act in different ways, such as changing the density dependency that maintains a strong resource partitioning (Stevens 2022c) or also facilitating the presence of new resource items that are shared between consumers (Manlick & Pauli 2020; Stevens 2022c). Although null models can be used to aid understanding whether the observed niche overlap is more or less than expected by chance, it is still difficult to infer what mechanisms are acting to create these patterns (Geange *et al.* 2011). It is also important to highlight that niche decomposition (OMI and WitOMI) proved to be an interesting tool to study bat DNs, showing details in the diets of the analysed species (Karasiewicz *et al.* 2017).

The observed results reinforce that the mechanisms that promote the high local diversity of fruit bats are probably a consequence of diet specialisation during high fruit abundance (Fleming 1993, Rex *et al.* 2010, Shipley & Twining 2020), leading to narrow niche breadth (Carlson *et al.* 2021). The adoption of more general feeding strategies in times of low food availability, leads to wider niches (Carlson *et al.* 2021, Sargeant 2007, Shipley & Twining 2020). In addition, the composition of the diet (based mainly on pioneer plants) shows the degree of disturbance in the region, and the need for strategies to reduce anthropogenic actions.

Thus, our research yielded remarkable information on the seasonality of bats diet and on how it affects food overlap among bat species. Using parameters like marginality and tolerance (WitOMI), we identified subtle seasonal differences which may not be noticed by comparing diets traditionally, as shown above. These findings contribute to understanding how bats species coexist, and

also in what way climate seasonality impacts on their diet and interactions. Besides, we highlight the necessity of carrying out further studies on TDFs, given that such environments have been scarcely explored and, consequently there is a lack of information on their ecology.

Finally, we shall state that, however, faecal analysis is a widely employed technique; it may have disadvantages when compared with DNA metabarcoding and isotopic composition investigation (Oliveira *et al.* 2022; Munoz-Lazo *et al.* 2019). These techniques show food items taken for long periods and not just those ingested during a unique consumption event (Schlautmann *et al.* 2021, Vizentin-Bugoni *et al.* 2021). Furthermore, the employment of additional methods, like direct observation and faecal sample collection where bats eat, as feeding roosts, may yield more data on consumption of fruit whose large seeds cannot be taken (epizoocoria). As a result, a broader understanding of the resources partition among bat species and their role on seed dispersal can be improved (Villalobos-Chaves & Rodrigues-Herrera 2021).

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