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ZOOLOGY

Frugivorous bat (Chiroptera: Phyllostomidae) community structure and trophic relations in Atlantic Forest fragments

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ABSTRACT. We evaluated the structure of a community of frugivorous bats using composition and abundance patterns, niche amplitude and food overlap of these animals in four Atlantic Forest fragments, each one exposed to different conservation realities. For twelve months, we captured six bat species and found the seeds of 13 species of pioneering plants in 158 fecal samples. The most abundant bat species were *Artibeus planirostris* (25.4%), *Artibeus lituratus* (24.1%) and *Carollia perspicillata* (23.9%). Only one fragment (Fazenda Unida), the most conserved area, exhibited a significantly different composition and abundance of species. We found low trophic niche amplitude values (<0.60), associated to high food overlaps. Our results suggest that bats can adjust their foraging strategy to deal with food availability variations. By favoring pioneering plant species, the fragmentation process noted of the studied areas creates an attractive environment for bats more tolerant to this type of disturbance. The sampled areas represent important secondary forest remnants in southern Brazil that require attention to avoid an even greater loss of bat diversity.

Keywords: bat assemblages; coexistence; diet analysis; forest fragmentation; species composition.

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Introduction

The fundamental niche of a species can be defined as a set of n-dimensions, where each dimension represents an important factor or resource in a multidimensional space (Hutchinson, 1957), considering interspecific interactions and abiotic conditions (Chase & Myers, 2011). Differentiation with regard to the use of one or more niche dimension, thus, becomes a determining factor for species coexistence and similar niche occupation (Hutchinson, 1957, Chesson, 1991). According to MacArthur and Levins (1967), there is a limit regarding how much species similarity can occur for them to coexist, since, otherwise, selective forces will exclude one of the competitors.

Certain factors, such as habitat heterogeneity, can aid in distinguishing niches and promote species coexistence (Chesson, 1994, Chesson et al., 2004, Hortal, Triantis, Meiri, Thébault, & Sfenthourakis, 2009). The term habitat heterogeneity is used to refer to the environmental variability within a certain an area, including topography, habitat type and vegetation structure (Tews et al., 2004, Hortal, Rodríguez, Nieto, & Lobo, 2008). Empirical evidence indicates positive correlations between habitat heterogeneity and species richness (Kohn & Walsh, 1994, Kerr & Packer, 1997, Triantis, Mylonas, Weiser, Lika, & Vardinoyannis, 2005, Juriado, Suija, & Liira, 2006, Hortal et al., 2009, Brown et al., 2013). However, due to increasing deforestation of tropical forests in the last 50 y (Gorresen & Willig, 2004, Peres et al., 2010, Ferreira et al., 2017), a decrease in species diversity is observed, especially species with higher habitat requirements (Hill et al., 2011). Vegetation loss, especially in agricultural areas, make habitats more homogeneous, resulting in loss of species (Foley et al., 2011).

In this context, animals that act as pollinators and seed dispersers in fragmented habitats are vital for biodiversity maintenance and ecosystem service provisions (Fleming & Heithaus, 1981, Estrada & Coates-Estrada, 2002, Gorresen & Willig, 2004, Cancio et al., 2016). Frugivorous bats are noteworthy in this regard, since they present characteristics that favour their success in accomplishing ecosystem services (Kunz, Torrez, Bauer, Lobova, & Fleming, 2011) and in the ability to colonize and survive in fragmented landscapes and agricultural mosaics (Bernard & Fenton, 2003, Cleary, Waits, & Finegan, 2016).

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Bats can occupy several trophic levels, ranging from primary to tertiary consumers (Krüger et al., 2014; Campbell, Nelson, Ogawa, Chikaraishi, & Ohkouchi, 2017) and exhibit the greatest feeding habit diversity among vertebrates (Simmons, 2005). This diversity allows them to occupy a wide range of niches (Pedro & Passos, 1995, Patterson, Willig, & Stevens, 2003, Lopez & Vaughan, 2007). Thus, knowledge on frugivorous bat species distribution in tropical forest fragments and their diets (including food overlap and food resource sharing) can aid in understanding their roles in these ecosystems (Vitt & Pianka, 2004). Therefore, the aims of the present study were to (1) evaluate the frugivorous bat community structure in Atlantic rain-forest fragments, by evaluating bat species composition and abundance patterns; and (2) investigate trophic niche amplitude and overlap among frugivorous bat species in the Upper Parana River Basin forest fragments.

Material and method

Study area

The study area encompassed a stretch of the Upper Paraná River, comprising a semideciduous seasonal forest, inserted near in large urban, industrial and agricultural centers (Lowe-McConnell, 1999). The entire Paraná River, including the studied region, presents seasonal floods in areas known as floodplains, which are subject to changes in biotic and abiotic characteristics due to routine flooding events (Agostinho & Zalewski, 1996, Thomaz, Bini, & Bozelli, 2007).

Bats were captured in four forest fragments, located in the states of Paraná and Mato Grosso do Sul (Figure 1): (1) Base (22°45′S, 53°15′W), a secondary forest area comprising approximately 1.7 ha; (2) Mutum Island (22°48′S, 53°13′W), a vegetated island that separates the main channel into secondary channels, c 15 km in length and width ranging from 500 to 1000 m (Corradini, Stevaux, & Fachini, 2008); (3) Mata do Araldo (22°47′S, 53°19′W), a riparian forest area, located on the left bank of the Paraná River, approximately 20 ha in size; (4) Fazenda Unida (22°41′S, 53°17′W), located on the right bank of the Baía River, one of the Upper Paraná River tributaries, area isolated by a matrix used to cultivate exotic fruits, comprising about 3.6 ha (Zanon & Reis, 2008).

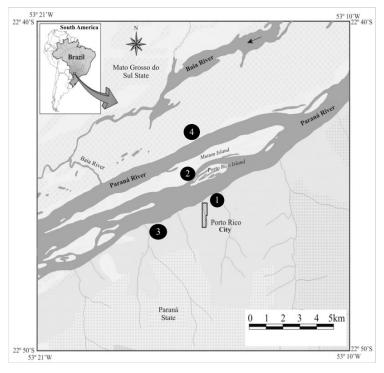


Figure 1. Map indicating the location of the Upper Parana River in Brazil, the river floodplain and its tributaries (in dark gray). The four Atlantic Rainforest fragments where bats were captured (solid light gray) were (1) Base, (2) Mutum Island, (3) Mata do Araldo and (4) Fazenda Unida. Hatched light gray areas represent the landscape matrix.

The Upper Paraná River floodplain vegetation, including the four fragments assessed herein, has suffered an accelerated devastation since the 70's. The vegetation has undergone a natural regeneration process from 1997 onwards, with the creation of the Environmental Protection Area comprising the Paraná River islands

and floodplains, currently representing a mosaic of forest patches of different ages (Cruz & Campos, 2015). Thus, each of the four fragments of this study are subject to different realities. Fragment 1, Base, is the most degraded and was formerly used for cattle grazing. This site is located near the Research Station of the *Universidade Estadual de Maringá* and subject to artificial illumination, due to the constant use of field station facilities into the evening hours (Souza et al., 2005). Fragment 2 is an island containing several forest fragments. This study focused on one comprising 1.5 ha. It displays an intermediate level of degradation, with the presence exotic species and fruit trees, such as guava (*Psidium guajava*, Myrtaceae), has been abandoned for some time and is in a more advanced stage of natural regeneration than the Base site. Fragment 3, Mata do Araldo, is a rare riparian forest fragment located on the left bank of the Upper Paraná River. Disturbances associated with selected tree harvesting, cattle entering the forest, and the presence of trails that lead to the river, are noted, but the forest along the river margin is in good state, and more preserved than Ilha Mutum. Fragment 4, Fazenda Unida, is less regularly access by people and is the best preserved of all four forest fragments.

Captures and data analyses

Captures were performed over 12 months, between January and December for one night each month at all four sites, beginning at dusk and ending at dawn. Due to the difference in the length of days and nights throughout the year (in the summer the days are longer and sunset occurs later, due to the summer solstices), the sampling time was not the same every month. Thus, the total capture time was equivalent to 136 h in each fragment, where bats were captured with the aid of 32 mist nets per night, (each net measuring $8.0 \times 2.5 \text{-m}$) with a total capture effort of $87,040 \text{ m}^2 \text{ h}$, according to Straube and Bianconi (2002).

The nets were set between 0.5 and 3.0 m from the ground to facilitate the capture of frugivorous phyllostomids that, due to the higher food availability in the region, are frequent in the sub-forest stratum (Carvalho, Fabián, & Menegheti, 2013). In addition, canopy feeding bats can also fly lower, especially when commuting between foraging sites to avoid predators (Rex, Michener, Kunz, & Voigt, 2011). The nets were positioned in forest clearings, quiet roads, trails and watercourses, and checked every 15 min. The data include both rainy and dry periods, to account for potential temporal variability in bat communities. We assumed that seasonality did not influence comparisons between species composition and abundance among fragments (Briones-Salas, Lavariega, & Moreno, 2017, Laurindo, Gregorin, & Tavares, 2017).

All captured bats were labelled with identification aluminium rings (Etiquetal-models 3.5 and 4.0) on their left forearm, allowing for the verification of possible recaptures. The captured bats were identified using the taxonomic descriptions reported by Emmons and Feer (1997), Dias, Peracchi and Silva (2002), Gregorin and Taddei (2002). Bats were kept inside cloth bags until defecation, and the feces were stored in plastic vials. Fecal samples from each individual were collected, separated and washed under running water. Initially, seeds were identified using a stereomicroscope, according to Lorenzi (2002). Subsequently, samples were verified by researchers and compared to material deposited at the *Universidade Estadual de Maringá* herbarium. In cases of any doubt, samples were sent to specialists. All procedures followed animal research guidelines approved by the *Universidade Estadual de Maringá* Ethics Committee (135/2012 - CEAE). The recapture rate over 12 months was low, so these data were not considered.

Two frugivorous bat community structure components were considered for the analysis, namely species composition and abundance. Bat community structure was evaluated by pattern variations in species composition (presence and absence of species among the evaluated fragments); where the matrix comprising multivariate species composition data was formed by four fragments (lines containing 12 months as sampling replicas for each fragment) and six frugivorous bat species (columns). Species abundance was given by catch per unit of effort; CPUE = N/A where N = total number of individuals and A = total area of mist nets, for each month, and the matrix comprised multivariate species abundance data (CPUE) in the four fragments (lines containing 12 months as sampling replicas for each fragment) with six species of frugivorous bats (columns). Differences in bat composition and abundance among forest fragments were tested by applying a Permutational Multivariate Variance Analysis - PERMANOVA with a repeated-measures design (Anderson, Gorley, & Clarke, 2008), where months were considered random effect to control the temporal data dependence. The forest fragments were considered factors (levels: Base, Mutum Island, Mata do Araldo and Fazenda Unida). The coefficient of dissimilarity metric applied in the PERMANOVA repeated-measures design concerning species composition was the Jaccard distance, and regarding species abundance, the Bray-

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Curtis distance. Post-hoc pairwise comparison tests were applied when significant differences were identified in species composition and abundance bats among fragments. P-values were obtained by the Monte Carlo test using 9999 permutations (Anderson, 2006). A significance level of α = 0.05 was applied. The PERMANOVA repeated-measures design analyses were performed using the PRIMER version 6.0 program (Anderson et al., 2008).

Trophic niche amplitude was calculated through the standardized Levins index (Hurlbert, 1978) (Equation 1):

Ba =
$$[(\Sigma_i Pij^2)^{-1} - 1] (n-1)^{-1}$$
 (1)

where: Ba is the amplitude of the standardized trophic niche; P_{ij} is the proportion of food item j in the diet of species I and n is the total number of food items.

This index ranges from 0 to 1, where values of 0 to 0.60 characterize an organism as a specialist and values above 0.60, as a generalist (Krebs, 1989).

Food overlap was estimated according to the Pianka index (1973), calculated with the aid of the EcoSim program: null model software for ecology, Version 7 (Gotelli & Entsminger, 2009), according to the following Equation 2:

$$O_{jk} = \frac{\sum_{i=1}^{S} P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^{S} P_{ij}^2 \sum_{i=1}^{S} P_{ik}^2}}$$
(2)

where: Ojk is the Pianka measure food overlap between species j and k; pij is the proportion of the food item i in the total of items used by species j; pik is the proportion of food item i in total of items used by species k, n is the total number of food items.

According to Gotelli and Graves (1996), this index measures the degree of food resource-sharing between two species on a scale of 0 to 1, where zero represents no overlap and one represents a total overlap.

Results

Frugivorous bat community structure

We captured 497 frugivorous bats comprising six species and four genera, all belonging to the Phyllostomidae family. The most common species were *Artibeus planirostris*, *Artibeus lituratus* and *Carollia perspicillata* (Table 1), which accounted for 73.4% of the total captured animals.

Table 1. Frugivorous bat species composition in four semi-deciduous seasonal forest fragments in the Upper Paraná River Basin - Brazil, captured between January and December 2006. BA = Base; IM = Ilha Mutum; MA = Mata do Araldo; FU = Fazenda Unida; N = total number of individuals captured during the study, with the percentage in parentheses. The list does not include recaptures.

Taxon	BA	IM	MA	FU	N(%)
Family Phyllostomidae					
Subfamily Carolliinae					
Carollia perspicillata (Linnaeus, 1758)	26	20	68	5	119(23.9)
Subfamily Stenodermatinae					
Artibeus fimbriatus Gray, 1838	5	3	8	16	32(6.4)
Artibeus lituratus (Olfers, 1818)	35	17	43	25	120(24.1)
Artibeus planirostris (Spix, 1823)	11	20	33	62	126(25.4)
Platyrrhinus lineatus (E. Geoffroy, 1810)	14	13	7	24	58(11.7)
Sturnira lilium (E. Geoffroy, 1810)	12	11	3	16	42(8.5)
Total number of individuals	103	84	162	148	497

Both the composition (PERMANOVA repeated-measures design; Pseudo - F = 3.12, P = 0.002) and abundance (PERMANOVA repeated-measures design; Pseudo - F = 3.79; P = 0.001) of bat species differed among the evaluated forest fragments (Table 2).

Table 2. Result of the post hoc statistical pairwise test used to indicate differences between four semi-deciduous seasonal forest fragments in the Upper Paraná River Basin, Brazil, concerning frugivorous bat species composition and abundance captured between January and December 2006.

Fragments —	Comp	oosition	Abuı	ndance
	t	P(perm)	T	P(perm)
Unida × Araldo	2.77	0.001	2.82	0.001
Unida × Mutum	2.03	0.014	2.08	0.019
Unida × Base	1.74	0.041	2.35	0.005
Araldo × Mutum	1.25	0.230	1.37	0.123
Araldo × Base	1.40	0.144	1.46	0.125
Mutum × Base	0.68	0.695	1.16	0.269

Frugivorous bat diet, amplitude and trophic niche overlap characterization

A total of 158 fecal samples containing seeds from 13 plant species belonging to four families (Piperaceae, Solanaceae, Moraceae and Urticaceae) were analyzed. Certain plant genera were ingested at higher rates by some bat species (Table 3).

Table 3. Number and percentages (in parentheses) indicate the seeds found in frugivorous bat faecal samples from four semideciduous seasonal forest fragments in the Upper Paraná River - Brazil.

Consumed seeds — (total item count)	Bat species						
	Artibeus lituratus	Artibeus fimbriatus	Artibeus planirostris	Carollia perspicillata	Platyrrhinus lineatus	Sturnira lilium	
Urticaceae							
Cecropia pachystachya (50)	4 (30.8)	5 (50)	14 (35.9)	10 (16.7)	12 (50)	5 (41.7)	
Moraceae							
Ficus adhatodifolia (22)	6 (46.1)		13 (33.4)		3 (12.5)		
Ficus eximia (9)	1 (7.7)	2 (20)	4 (10.3)	1 (1.7)		1 (8.3)	
Ficus luschnathiana (1)			1 (2.5)				
Ficus pertusa (5)			3 (7.7)		2 (8.3)		
Piperaceae							
Piper amalago (8)			1 (2.5)	7 (11.7)			
Piper amplum (39)	2 (15.4)	3 (30)	3 (7.7)	23 (38.3)	4 (16.6)	4 (33.4)	
Piper crassinervium (3)				2 (3.3)	1 (4.2)		
Piper macedoi (2)				2 (3.3)			
Piper tuberculatum (12)				12 (20)			
Solanaceae							
Solanum paniculatum (2)				1 (1.7)	1 (4.2)		
Solanum granuloso (4)				2 (3.3)	1 (4.2)	1 (8.3)	
Solanum viarum (1)						1 (8.3)	
∑(%)	13 (100)	10 (100)	39 (100)	60 (100)	24 (100)	12 (100)	

Cecropia pachystachya and Piper amplum were the only fruits consumed by all bats. None of the Artibeus species consumed Solanum fruits, so this group was less consumed by the evaluated bats. Cecropia pachystachya was the most consumed food item, representing most of the diet of four bat species (A. fimbriatus, A. planirostris, P. lineatus, S. lilium). Although Piper amplum fruits were consumed by all bat species, C. perspicillata displayed a higher preference for this species.

The presence of dominant items in the bat diets suggests a more restricted diet, evidenced by low trophic niche amplitude values (<0.60). However, variations among the index of each species may provide more clues as to bat feeding habits. Among the captured bats, *C. perspicillata* (Ba = 0.28) and *A. planirostris* (Ba = 0.23) presented the highest niche amplitude indices, indicating that they consume a greater diversity of food items than the other evaluated bat species. *Artibeus fimbriatus* (Ba = 0.14) and *A. lituratus* (Ba = 0.16) displayed the lowest niche amplitude indices, while *Platyrrhinus lineatus* (Ba = 0.19) and *Sturnira lilium* (Ba = 0.19) presented intermediate trophic niche amplitude values.

No total diet overlap for the bats captured in the four evaluated forest fragments was detected. However, high overlap values were observed between *A. fimbriatus* and *S. lilium* (O = 0.96), followed by *A. lituratus* and *A. planirostris* (O = 0.95) and, finally, *A. fimbriatus* and *P. lineatus* (O = 0.88). The lowest values were detected for *C. perspicillata* and *A. planirostris* (O = 0.37), followed by *C. perspicillata* and *A. lituratus* (O = 0.39).

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Discussion

Seasonal forests are among the most endangered phytophysiognomies on the planet (Miles et al., 2006), and Atlantic Forest remnants follow this pattern, being severely degraded throughout their natural occurrence, mainly due to farming practices and the expansion of agricultural activities (Durigan, Franco, Saito, & Baitello, 2000). The low number of species captured herein reflects part of this threat, since the four studied fragments exhibit characteristics that compromise the presence of more sensitive animals, such as small sizes and exposure to disturbances. The bat captures represented 3.4% of the 178 bat species recorded in Brazil (Nogueira et al., 2014) and 9.5% of the 63 species recorded in the studied area (Miretzki & Margarido, 1999, Miretzki, 2003, Bianconi, Mikich, & Pedro, 2004, Ortêncio-Filho et al., 2005, Ortêncio-Filho & Reis, 2009, Silva, Ortêncio-Filho, & Lacher, 2013).

In this study, three phylostomids, *Artibeus planirostris*, *A. lituratus* and *Carollia perspicillata*, were numerically dominant in the sample area. Considered common in the neotropics (Pedro, Passos, & Lim, 2001, Silveira et al., 2011, Carvalho-Ricardo, Uieda, Fonseca, & Rossi, 2014), these frugivorous species represent most of the captures in seasonal Paraná forests (Muller & Reis, 1992, Reis, Peracchi, & Onuki, 1993, Reis, Peracchi, & Sekiama, 1999, Sekiama, Reis, Perachi, & Rocha 2001, Miretzki, 2003), indicating that they exhibit lower sensitivity to degraded areas. This is in agreement with other studies, where species belonging to the *Artibeus* and *Carollia* genera are commonly reported as the most abundant in disturbed areas, since they present great food plasticity and make use of shelters (Novaes & Nobre, 2009, Ferreira, Fischer, & Pulchério-Leite, 2010, Silva & Anacleto, 2011, Silveira et al., 2011, Munin, Fischer, & Gonçalves, 2012, Prone, Zanon, & Benedito, 2012, Gazarini & Pedro, 2013, De la Peña-Cuéllar, Benítez-Malvido, Avila-Cabadilla, Martínez-Ramos, & Estrada, 2015).

The bat species captured herein presented restricted diets, confirmed by low trophic niche amplitude values, thus considered specialists. However, it is better to describe them as punctual specialists, since a restricted diet does not always indicate specialization. A species can be induced to consume a particular source of food that is temporarily abundant in the environment (Silva, Gaona, & Medellín, 2008, Teixeira, Corrêa, & Fischer, 2009, Dias, Ortega, Gomes, & Agostinho, 2017), which is probably the case of the bats caught in our sampled area. The results indicate no diet segregation, with high food overlap among five species (*Artibeus fimbriatus*, *A. lituratus*, *A. planorostris, Sturnira lilium* and *P. lineatus*). Munin et al., (2012) reported similar results, for Phyllostomidae in the Pantanal, with high overall dietary overlap for more commonly available foods. This may may reflect the fragmented environment the sampled areas are inserted in, whith few abundant food items and species adapted to this reality. Laurindo, Novaes, Vizentin-Bugoni, & Gregorin (2018) demonstrated that fruit bat diets in fragmented areas are less diverse than in large forest fragments.

The four plant families observed herein are characterized as pioneer species (Piperaceae, Solanaceae, Moraceae and Urticaceae) and are widely consumed by frugivorous bats (Lobova, Geiselman, & Mori, 2009). In general, fruits belonging to these genera (*Piper, Solanum, Ficus* and *Cecropia*) display characteristics that fit dispersion performed by these mammals, known as chiropterocoria, such as fleshy fruits that do not change color from the green phase to mature, attractive aromatic substances when ripe and exposed location in tree or plant branches (Van der Pijl, 1982). This strengthens the evidence that bats are extremely important in the regeneration of degraded environments, as reported by De La Peña-Domene, Martínez-Garza, Palmas-Pérez, Rivas-Alonso, & Howe (2014).

The evaluated bat assembly seems to share food resources, with evidence of a specialist diet regarding certain plant groups. An observed preference for *Sturnira lilium* differs from other published studies, since greater consumption of species belonging to the *Solanum* and *Piper* genera is usually reported (Giannini & Kalko, 2004, Sánchez, Giannini, & Barquez, 2012). However, in the present study, higher *Cecropia* consumption rates were observed, although *Piper* consumption was also significant. This confirms the aforementioned hypotheses that, due to the few abundant food items in the sampled area, local bat species are adapted to this reality. Therefore, *Sturnira* interactions with *Solanum* should not be generalized, as they may vary according to specific characteristics in the sampled area. Some studies have also reported these variations concerning *Sturnira* preference according to specific geographic locations (Sánchez & Santos, 2015) and latitude variations (Saldaña-Vázquez, Sosa, Iñiguez-Dávalos, & Schondube, 2013).

Among the captured species, *Carollia perspicillata* and *A. planirostris* presented the highest simultaneous niche amplitude values and a low food overlap, indicating that their diet is not concentrated only on a few

resources and that segregation regarding food item consumption exists. This allows these species to coexist in great abundance and justifies their high representativeness in this study. Smaller niche amplitudes were observed for *A. fimbriatus* and *A. lituratus*, indicating that these species display more restricted feeding habits in certain situations. This may be due to many factors, since variations among individuals associated with sex, age and behavioral mechanisms may occur (Bolnick et al., 2003; Bobrowiec & Cunha, 2010). In addition, changes in food availability and diversity during specific times of the year may lead to specialist behavior in some species (Bolnick et al., 2003), narrowing their trophic niche. Although further research is required, these results may also represent a narrowing concerning the preference for *Cecropia* and *Ficus*, which has been previously documented (Andrade, Thies, Rogeri, Kalko, & Mello, 2013) since the bats did not consume available *Solanum* items in the studied forest fragments.

The highest food overlaps were observed between *A. fimbriatus* and *S. lilium* and *A. lituratus* with *A. planirostris*, indicating that these species are competing for the same food resources on a local scale. The results differ from those reported by Amaral, Macário and Aguiar (2016) in a Neotropical savanna, where they suggest that *A. lituratus* and *A. planirostris* do not compete with each other. These data indicate that bats can eat alternative items during lower availability of preferential fruits. This situation was also observed by Ramos-Pereira, Marques and Palmeirim (2010) and can be associated to habitat loss and fragmentation, which leads to changes in the structure and stability of the interaction networks (Laurindo et al., 2018). Thus, it is understandable that competitions that would probably not occur in non-fragmented environments may be in place.

Although indications of local competition were noted, frugivorous bats presented a greater trophic niche overlap, consuming mainly *Cecropia* (*A. fimbriatus*, *S. lilium*, *A. planirostris*) and *Ficus* (*A. lituratus*) items, which are abundant in degraded areas. Since these are pioneer plants, characterized by rapid growth, and display advantages in edge areas, clearings and disturbed environments, these genera are abundant in the evaluated forest fragments, and their high fruit availability can allow for bat coexistence without major losses. In addition, caution must be applied when determining the different situations and scenarios in which interspecies competition occurs or does not occur, since Salinas-Ramos, Ancillotto, Bosso, Sánches-Cordero and Russo (2019) consider that, in some cases, limited resources are synonymous with competition.

Considering the evaluated objectives and the frugivory results of the present study, the bat assembly in the studied forest fragments at the Paraná River presented similar species composition and abundance, except for Fazenda Unida, which is more preserved compared to the other fragments. The low trophic niche amplitude values associated with high food overlap suggest that bats can make adjustments in their foraging strategies to deal with food supply variations.

Conclusion

By favouring pioneer species, the fragmentation process in the studied area creates an attractive environment for bats more tolerant to this disturbance, indicating a reality of both limited and abundant food items. The results confirmed this opportunistic aspect of certain frugivorous bats in disturbed environments and indicates biodiversity risks in these areas, as a low number of species was captured. This reality may be occur in fragments displaying similar characteristics to the present study, mainly degradation.

The sampled fragments represent important secondary forest remnants in southern Brazil that require attention. Investments in conservation strategies, such as matrix management through quality improvement (Farneda et al., 2015), should be considered in order to avoid even greater loss of bat diversity.

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