THERYA, 2023, Vol. 14(3):383-394 DOI:10.12933/therya-23-4914 ISSN 2007-3364

Chiropteran diversity and diet of fruit bats in a tropical dry forest of northern South America

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Remnants of Tropical Dry Forest persist in urban and peri-urban areas and are essential for maintaining biodiversity and ecosystem services. However, the challenges facing the conservation of these respective forests have intensified with the encroachment of the urban frontier, mining activities, deforestation, and cattle ranching. In this context, our study aims to estimate the diversity of the order Chiroptera and characterize the diet of the family Phyllostomidae. This approach allows us to gain insights into the ecological dynamics and assess the status of Tropical Dry Forest fragments located within the urban and peri-urban areas of Cúcuta, Colombia. Field sampling was conducted from January to September 2018, with a total sampling effort of 2,160 hours/meter/net. Bats were sexed, morphometrically characterized, and had their feces collected for diet analysis before being tagged and released. We identified three families, nine genera, and 11 species. A total of 276 individuals were captured. Seven species were observed in the urban area and ten in the peri-urban zone; *Artibeus lituratus* and *Carollia perspicillata* were the most abundant species in both locations. The diet included seeds from the families Moraceae, Anacardiaceae, and Rosaceae. Our findings reveal that in areas with dense vegetation, such as peri-urban zones, frugivorous bats prefer to consume fruits of domesticated species, including economically significant fruits like guava and tomato. This dietary shift could alter seed dispersal patterns and the dynamics of the Tropical Dry Forest, highlighting the ecological importance of these flying mammals in ecosystem regeneration.

En las zonas urbanas y periurbanas, perduran fragmentos de bosque seco tropical que desempeñan un papel fundamental en la conservación de la biodiversidad y los servicios ecosistémicos. Sin embargo, los desafíos para preservar estos remanentes forestales han aumentado debido al avance de la urbanización, la minería, la deforestación y la ganadería. En este contexto, nuestro estudio tiene como objetivo estimar la diversidad del Orden Chiroptera y caracterizar la dieta de la familia Phyllostomidae como una estrategia para comprender las dinámicas ecológicas y evaluar la situación de los fragmentos de bosque seco tropical situados en el área urbana y periurbana de Cúcuta, Colombia. Llevamos a cabo muestreos de campo durante los meses de enero a septiembre de 2018, con un esfuerzo de muestreo total de 2,160 horas/metro/red. Los murciélagos fueron sexados, caracterizados morfo-métricamente, y se tomaron muestras de heces para determinar su dieta antes de ser marcados y liberados. Se capturó un total de 276 individuos, Identificamos tres familias, nueve géneros y once especies de murciélagos. Encontramos siete especies en el fragmento urbano y diez en la zona periurbana, con *Artibeus lituratus* y *Carollia perspicillata* siendo las especies más abundantes en ambos sitios. En cuanto a la dieta, se obtuvieron semillas de las familias Moraceae, Anacardiaceae y Rosaceae. Nuestros hallazgos revelan que, en áreas con mayor cobertura vegetal como zonas periurbanas, los murciélagos frugívoros prefieren frutos de especies domesticadas, incluyendo frutas de relevancia económica como guayaba y tomate. Esta tendencia dietética podría alterar la dispersión de semillas y la dinámica del Bosque Seco Tropical, subrayando la importancia ecológica de estos mamíferos voladores en la regeneración del ecosistema.

Keywords: Abundance; bioindicator; Colombia; peri-urban; Phyllostomidae; urban ecology.

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Introduction

Tropical dry forests (TDF) represent valuable biodiversity reservoirs linked to essential ecosystem services, including water, recreational, and genetic resources (Pizano and García 2014). Globally, TDFs cover an impressive 42 % of the total area of tropical forests (Quesada *et al.* 2009). However, the extent of these forest remnants has been severely reduced due to multiple factors, including the expansion of urban areas, mining activities, deforestation, and livestock raising, in sharp contrast to adjacent biomes like Andean forests. These anthropogenic pressures have sculpted the TDF landscape, posing a significant risk to biodiversity and the ecological interactions they support (Miles *et al.* 2006). As a result, TDFs are considered one of the most threatened biomes, facing the loss of biodiversity, decline of genetic diversity, and fragmentation of landscape connectivity, resulting in isolated mosaic patterns and the risk of local extinctions (Pizano and García 2014).

In Colombia, TDFs historically cover a wide geographic range, estimated at approximately 80,000 km^2 (Pizano and García 2014). However, these forests currently cover only 8 % of their original extent (Garcia et al. 2014). The areas once covered by TDF have been converted to urban areas, forest remnants, and agricultural (28 %) and livestock (34 %) production areas (Etter 2008; Pizano and García 2014).

In the Norandina region of Colombia, about 47 % of the 80,000 km² identified as TDF correspond to natural fragments, while the remaining 53 % is dedicated to agricultural and livestock activities that still conserve small remnants of secondary forest (Garcia et al. 2014). This situation has led to substantial changes in the spatial configuration of the available habitats at the local landscape level, exerting apparent effects on the abundance and diversity of the regional fauna and flora.

In Colombia, bats play a central role, representing 30.9 % of the mammal richness in the country, with a total of 217 species. This positions Colombia as the second most chiropteran- diverse country worldwide, after Indonesia (Ramírez-Chaves *et al.* 2021). In the context of the Neotropics, Colombia is a leading country in number of bat species, surpassing countries such as Brazil (182), Ecuador (178), and México (140; Ceballos and Arroyo-Cabrales 2012; Abreu *et al.* 2022; Tirira *et al.* 2022). Bats, being more numerous than other mammal groups, play a central role in multiple ecosystem processes and are of particular interest in the analysis of environmental changes in ecosystems (Jones *et al.* 2009). Some authors have formulated the idea that variations in the diversity and composition of bat populations may be influenced by food availability and the preservation of their environments (Medellín *et al.* 2000; Chávez and Ceballos 2001; Jiménez-Ortega and Mantilla-Meluk 2008). This is due to the close relationship of bats with particular groups of plants; for example, they participate in the pollination of dozens of plants and control of insect populations, besides playing a major role in seed dispersal (Medellín *et al.* 2000; Willig *et al.* 2007; Ávila-Cadabilla *et al.* 2009).

Despite the continuous degradation of TDFs in Colombia (MINAMBIENTE 2021) and the importance of bats in diagnosing the state of ecosystems (García-Morales *et al.* 2013), little is known about the ecology of bats in northeast Colombia. The studies on TDFs include those conducted in Área Natural Única Los Estoraques (ANULA), which report a list of seven bat species (Anteliz-Pallares *et al.* 2021), the use of shelters by three species of phyllostomid bats (Suárez-Payares and Lizcano 2011), and aspects associated with the diet (Alviz and Pérez-Torres 2020), and body size (Acevedo and Pabón 2020).

Although studies have been conducted on bat assemblages associated with anthropogenic disturbances, most have focused on evaluating the effects of habitat fragmentation associated with the establishment of agricultural, extensive livestock and silvo-pastoral systems (Estrada and Coates-Estrada 2001; Numa *et al.* 2005; Ortegón-Martínez and Pérez-Torres 2007; Vela- Vargas and Pérez-Torres 2012). The resulting changes in the structure and composition of bat assemblages in TDF fragments occupied by urban settlements are unknown. A study by Ramos (2021) addressed the effects of habitat reduction on species richness and abundance of phyllostomid bats in TDF fragments of the Colombian Caribbean zone. This study reported that the ecological effects of habitat fragmentation and loss in bats are species-specific, which could lead to the local extinction of some species while being beneficial or may not affect others.

Most studies on habitat loss have evaluated its effect according to fragment size (Santos and Telleria 2006), finding that species diversity and abundance increase in larger fragments that offer greater resource availability (Mena 2010). Habitat reduction is clearly one of the anthropic processes with the greatest effects on biodiversity (Santos and Tellería and Santos 2006). However, the responses can differ according to the particular ecology of the species (Mena 2010; Cabrera 2011).

In a context of high anthropic disturbance, such as the one observed in the TDF in the Cúcuta metropolitan region (Norte de Santander, Colombia), examining the impacts of habitat reduction on the diversity and diet of animal species has become imperative. Therefore, we first carried out a comprehensive description of the bat diversity and composition, classifying them into guilds and covering all possible families. Subsequently, we analyzed the diet composition of frugivorous bats of the family Phyllostomidae in two TDF fragments immersed in urban and peri-urban areas.

The central hypothesis of this study was that habitat reduction caused by human activities in the urban area has impacted both the diversity of chiropterans from different guilds and the availability of food resources used by the family Phyllostomidae, compared to peri-urban fragments. This process led to substantial modifications in the diversity and abundance of bat species inhabiting these areas. This study aims to provide key information for biodiversity conservation in the Cúcuta Tropical Dry Forest, highlighting the importance of protecting and restoring habitats in urban and peri-urban areas. By understanding how anthropogenic disturbance impacts bat diversity and diet, we hope to contribute to implementing effective conservation strategies that promote the coexistence of these key species in these ecosystms.

Materials and methods

Study area. The study was carried out in two TDF fragments of the municipality of Cúcuta, Norte de Santander, Colombia: 1) TDF peri-urban fragment located on the outskirts of the Cúcuta City urban zone in the corregimiento of San Pedro (7° 48' 17.0'' N, -72° 31' 32.5' W), comprising an area of 23,289 m² with secondary (*e. g.*, *Licania apetala*) and atypical (*e. g.*, *Ficus carica* L., *Solanum lycopersicum*) plant species. 2) TDF urban fragment located among urbanized areas in the EcoParque theme park, one of the largest green areas in Cúcuta City (7° 51´51.8" N, -72° 30´ 24" W), comprising an area of 20,939 m²; the TDF fragments are highly altered, and largely comprise dry scrub vegetation (Figure 1). The study areas have an average elevation of 300 masl, characterized by a warm climate, with mean annual temperature of 25 °C, annual relative humidity of 75 %, and mean annual precipitation of 867 mm to 2,063 mm.

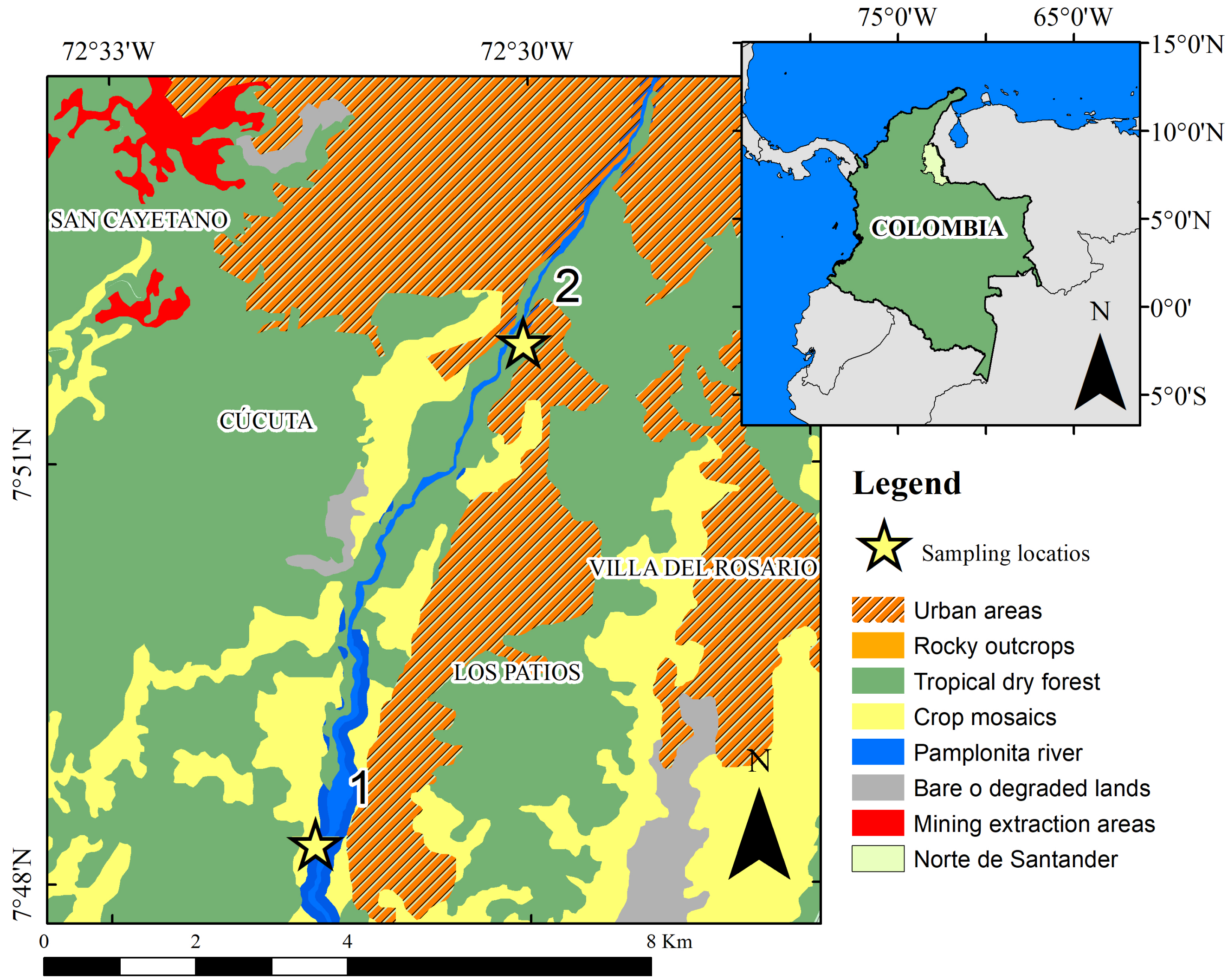

Figure 1. TDF fragments selected for the present study in the Cúcuta metropolitan area, Colombia. 1) Peri-urban zone. 2) Urban zone.

Field data collection. We conducted a general survey of the plants in the fragments studied, capturing photographic records and collecting samples of plants with fruits for subsequent identification to obtain general information on the food resources available to the bat community. Plant species were identified using the taxonomic keys of Linares and Moreno (2010) by comparison with plant specimens deposited in the botanical collection of the Catatumbo Sarare Regional Herbarium (HECASA) at Universidad de Pamplona.

Eight field trips were carried out between January and September 2018, each lasting 16 nights in each TDF fragment. Bats were captured using two mist nets measuring 12 m long by 3 m high, with 15 mm x 15 mm mesh size, which were kept open between 18:00 and 24:00 and reviewed every 10 to 15 minutes. In each sampling campaign, full-moon nights were avoided to the extent possible because they may affect bat capture due to lunar phobia (Santos-Moreno *et al.* 2010). All captured individuals were weighed, and their morphometric measurements were recorded for identification following the guidelines of Díaz *et al.* (2011). To avoid re-sampling, each captured bat was marked using a four-digit X 3/8" Lhaura® tattoo machine and released in places adjacent to the study area. Specimens were collected under the research framework license number 200 granted by the Corporación Autónoma Regional de la Frontera Nororiental (CORPONOR, in Spanish) to the Universidad de Pamplona. Specimens were preserved following the protocols of Simmons and Voss (2009) and were deposited in the mammal collection of the "José Celestino Mutis" Museum of Natural Sciences at the Universidad de Pamplona.

Seeds consumed by phyllostomid bats. The captured bats were placed in cloth bags to subsequently take fecal samples, which were stored in Eppendorf tubes with 70 % alcohol for preservation. The seeds and plant remains were separated with tweezers and distilled water under a Carl Zeiss stereo microscope; then, these were dried at room temperature (Ríos-Blanco and Pérez-Torres 2015). Seeds were identified by comparison against HECASA specimens, botanical samples, and photographic records captured in the sampling area. Plant species were identified using the guide for the taxonomic identification of seeds of Dueñas *et al.* (2011).

Data analysis – diversity. The relative abundance of bat species in the urban and peri-urban areas was estimated by constructing rank-abundance curves, transforming the values to log10 (Magurran and Henderson 2011). We used sampling completeness with the true diversity estimator based on Hill numbers (Chao and Jost 2012; Chao *et al.* 2014). This estimator is based on the species with one and two samples relative to the total abundance of individuals (Ortiz and Henao 2014). To know the percentage of completeness of the sampling, the "sample coverage" technique was performed, which calculates the proportion of each species in the sample relative to the total number of individuals through the standardization of the communities sampled (Chao and Jost 2012; López-Mejía *et al.* 2017). The analysis was performed with the iNEXT package (Hsieh *et al.* 2016) in R v. 3.6.3 (R Core Team 2013). The diversity of three orders was calculated (Jost 2007): 1) Order ^{0}q, representing the species richness or total number of species. 2) Order ^{1}q, based on the exponential Shannon index, which weights the most common species. 3) Order ^{2}q, based on the inverse Simpson index associated with abundant species.

Beta diversity was estimated through a dissimilarity analysis using Sorensen's index ($Ss = 2a/[2a + b + c]$), where a = number of common species; b = number of unique species occurring only at site one; c = number of unique species occurring only at site two (Koleff *et al.* 2003). The data were analyzed with the betapart package (Baselga and Orme 2012) in R v. 3.6.3 (R Core Team 2013).

Diet. The diet of phyllostomid bats was determined through the following parameters. 1) The absolute frequency of seeds (FA) based on the number of times a seed type was recorded in all the feces obtained per individual collected. 2) The percentage of occurrence (PO) for each seed species, obtained using the ratio of the absolute frequency (FA) relative to the total number of feces: $(PO) = (FA)/\text{Total number of feces} \times 100$; Kunz and Whitaker 1983). We assumed that the number of times a seed is found in the feces indicates its importance in the diet of bats. In addition, direct observations were made of the direct consumption of fruits of some species not usually recorded in the diet of these species.

Importance as seed dispersers. The importance of each frugivorous bat as a seed disperser in each community was evaluated with the Disperser Importance Index (DII; Galindo-González *et al.* 2000). This index uses the relative abundance of each captured bat species (B) and the percentage of feces samples containing seeds from each bat species (S). Samples with at least one seed were counted as one event, samples with two different seed species were counted as two events, and so on. $DII = (S*B)/1{,}000$. The index ranges between a minimum value of 0 (zero), indicating seedless feces (rare bat species dispersing a few seeds will have values close to zero), and a maximum of 10, indicating that a bat species disperses all seeds from a particular plant in the community.

Results

A total of 276 individuals distributed in three families, nine genera, and 11 species were recorded (Figure 2, Table 1) using a sampling effort of 2,160 hours/meter/net, corresponding to 90 hours over sixteen nights, for successful capture of 0.1255 individuals/hour/meters/net.

In the peri-urban area, we collected 164 individuals belonging to ten of the 11 bat species found in the study. According to the rank-abundance curve (Figure 3), the following categories were observed: Rare species: *Desmodus rotundus* (0.6 % of the captured species) and *Pteronotus parnellii fusco* (0.6 %). Moderately abundant: *Platyrrhinus fusciventris* (4.2 %), *Sturnira lilium* (1.8 %), *Glossophaga soricina* (3.6 %), *Carollia brevicauda* (4.2 %), and *Myotis nigricans* (2.4 %). Abundant: *Artibeus lituratus* (43.2 %), *Carollia perspicillata* (33.5 %), and *Uroderma bilobatum* (5.4 %). Of the ten species recorded, 60 % belong to the frugivorous guild, 20 % to the arthropodophagous guild, and 10 % to the nectarivorous and hematophagous guilds (Table 1).

In the urban area, we collected 112 individuals belonging to seven of the 11 bat species recorded in the study. The only rare species was *C. brevicauda* (0.8 %). Moderately abundant: *G. soricina* (5.3 %), *Artibeus obscurus* (5.3 %), and *S. lilium* (2.6 %). Abundant: *A. lituratus* (52.6 %), *C. perspicillata* (24.1 %), and *U. bilobatum* (8.9 %). Regarding guilds, the study recorded that 85.7 % of the seven species corresponded to the frugivorous and 14.7 % to the nectarivorous guilds (Table 1).

The sampling completeness in the urban and peri-urban areas recorded values of 95 %. The species richness in the sampled areas showed that the peri-urban area obtained the highest richness, with ten species, followed by the urban area, with seven species (Figure 4).

Table 1. Relative abundance of each species in urban and peri-urban TDF fragments in the Cúcuta metropolitan area, Norte de Santander, Colombia. Each species are classified according to its guild. A = arthropodophagous, F = frugivorous, H = hematophagous, and N = nectarivorous. Habitat type: urban fragments (UF) and peri-urban fragments (PUF).

Bat species	Guild	UF	PUF
Family Phyllostomidae			
Artibeus lituratus	F	59	71
Artibeus obscurus	F	6	0
Carollia perpicillata	F	27	55
Platyrrhinus fusciventris	F	0	7
Glossophaga soricina	N	6	6
Carollia brevicauda	F	1	7
Sturnira lilium	F	3	3
Desmodus rotundus	H	0	1
Uroderma bilobatum	F	10	9
Family Vespertilionidae			
Myotis nigricans	A	0	4
Family Mormoopidae			
Pteronotus parnellii fusco	A	0	1
Total		112	164

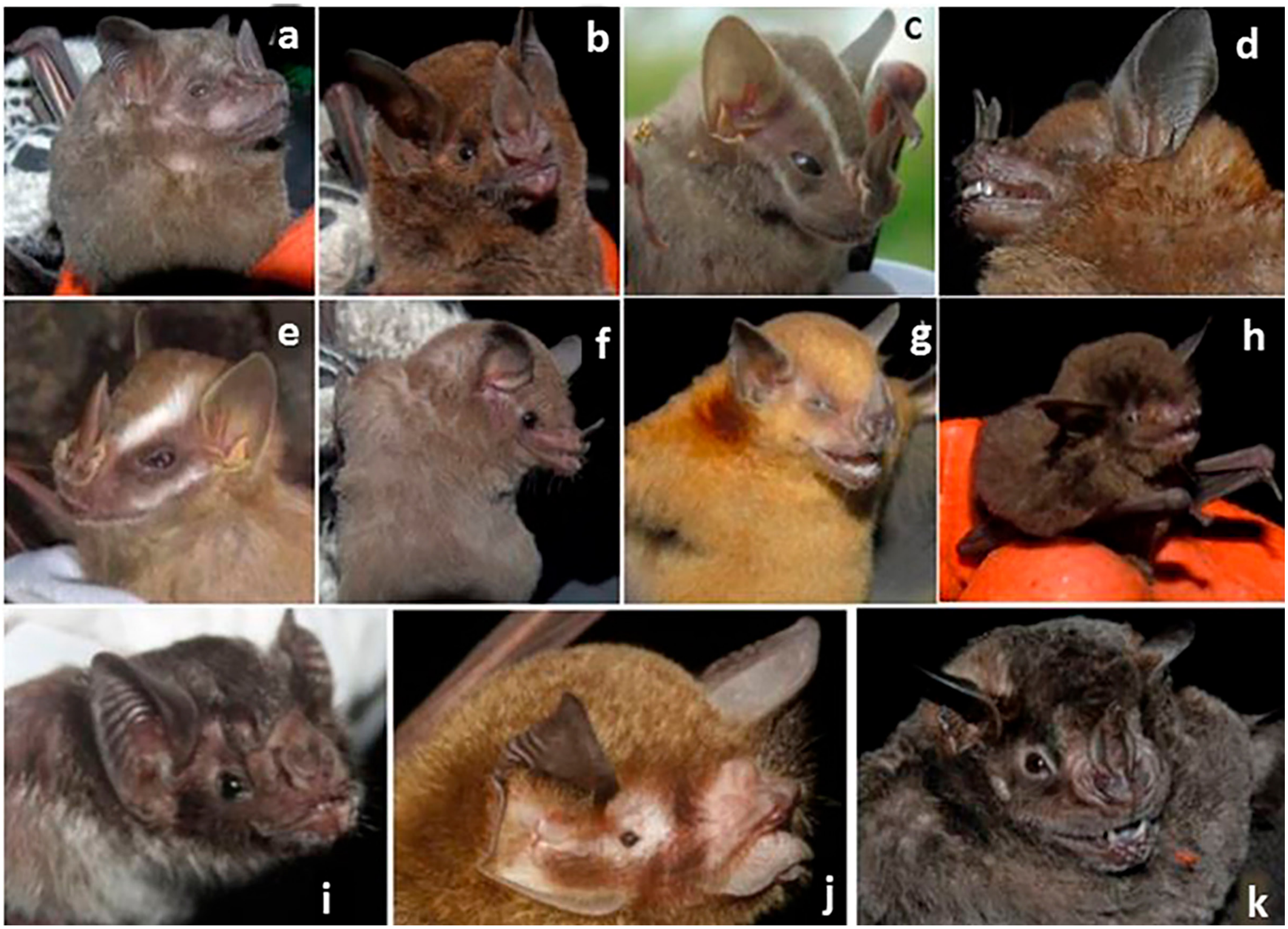

Figure 2. Bat species recorded in the peri-urban and urban TDF fragments studied. (a) *Artibeus lituratus*, (b) *Carollia perspicillata*, (c) *Uroderma bilobatum*, (d) *Carollia brevicauda*, (e) *Platyrrhinus fusciventris*, (f) *Glossophaga soricina*, (g) *Sturnira lilium*, (h) *Myotis nigricans*, (i) *Desmodus rotundus*, (j) *Pteronotus parnellii fusco*, and (k) *Artibeus obscurus* (Photographs a–j by Friedman Pabón and k by Roberto L. Morim).

For the diversity of order ^1q, the peri-urban area had the highest number of common species, with 4.50 effective species, compared to the urban zone, which reported 3.85. For order ^2q, the peri-urban area recorded the highest number of dominant species, with 3.23 effective species, having 1.13 times more dominant species than the urban zone, which reported 2.85 effective species (Figure 5).

The beta diversity estimated by the Sorensen index showed that the two communities (urban and peri-urban) may correspond to the same chiropteran assemblage with a variation between 0.2 and 0.6. However, some species were only recorded in a single community (peri-urban: *P. fusciventris, M. nigricans, P. parnellii fusco*, and *D. rotundus*; Urban: *A. obscurus*; Figure 3)

Percentage of occurrence (PO) of fruits consumed by bats. For the urban area, 49 feces samples were collected from five species of phyllostomid bats. In total, five types of plants were recorded from seeds (four at the species level; Table 2). The fruits with the highest percentage of occurrence in the diet of *A. lituratus* were *Ficus obtusifolia* (fig), with 40 %, and *Piper aduncum* L. (cordoncillo), with 30 % (Table 2). For *C. perspicillata*, the seeds of *F. obtusifolia* and *Cecropia* sp. (yarumo) showed the highest occurrence in their diet, with 55.6 % and 50 %, respectively. *Uroderma bilobatum* feeds on the fruits of four plant species, namely, *F. obtusifolia*, with a 50 % occurrence in its diet, followed by fruits of *Cecropia* sp., *P. aduncum*, and *Psidium guajava* (guava), which showed a 33.3 % occurrence. *Glossophaga soricina* consumed two types of fruits, where the seeds of *Cecropia* sp. showed a 33.3 % occurrence in the diet and *P. aduncum*, with 66.7 % occurrence. On the other hand, *S. lilium* consumed *F. obtusifolia* and *P. aduncum*, with frequencies of 50 % and 100 %, respectively. Additionally, direct field observations recorded the consumption of *Mangifera indica* (mango) fruits by *C. perspicillata*.

For the peri-urban area, 87 feces samples were collected from seven species of phyllostomid bats. A total of five seed species were recorded (Table 2). The seeds with the highest percentage of occurrence in the diet of *A. lituratus* were *F. obtusifolia* (50 %) and *Cecropia* sp. (40.6 %). *Carollia perspicillata* recorded the consumption of five types of seeds, where *Solanum lycopersicum* (tomato) and *F. obtusifolia* (fig) were the fruits with the higher occurrence in their diet, with 41.7 % and 33.3 %, respectively (Table 2). For

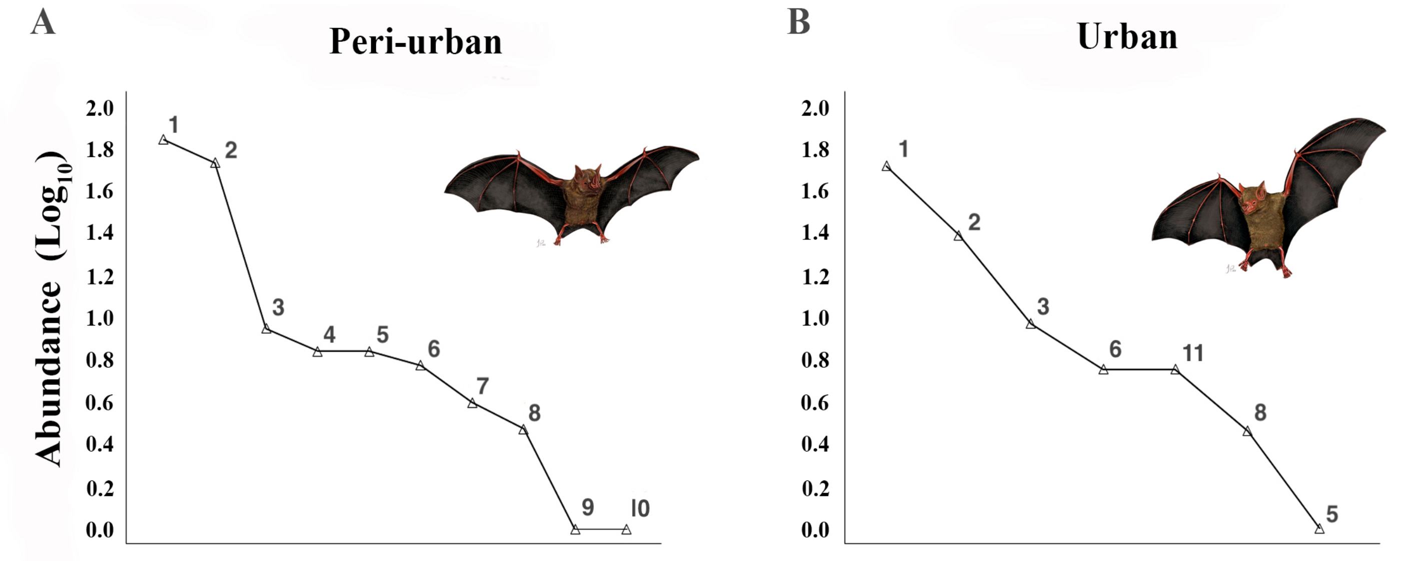

Figure 3. Abundance distribution plots for bat species in the urban and peri-urban TDF fragments in the Cúcuta metropolitan area, Colombia. *Artibeus lituratus* (1), *Carollia perspicillata* (2), *Glossophaga soricina* (3), *Platyrrhinus fusciventris* (4), *Carollia brevicauda* (5), *Uroderma bilobatum* (6), *Myotis nigricans* (7), *Sturnira lilium* (8), *Pteronotus parnellii fusco* (9), *Desmodus rotundus* (10), and *Artibeus obscurus* (11).

G. soricina, the seed with the highest percentage of occurrence was *P. aduncum,* with 66.7 %, while *S. lilium* recorded three seed species with the same proportion (*F. obtusifolia, P. aduncum,* and *S. lycopersicum*), with 33.3 %. *Uroderma bilobatum* feeds mainly on *F. obtusifolia,* with 80 %. *Carollia brevicauda* feeds on three types of fruits, mainly *S. lycopersicum* (75 %). Finally, *P. fusciventris* feeds mainly on *F. obtusifolia,* with 66.7 %. On the other hand, direct field observations recorded the consumption of *Manilkara zapota* (zapote) and *Mangifera indica* (mango) fruits by *A. lituratus* (Table 2).

Disperser importance index (DII). The values of the disperser importance index for the peri- urban area (DII = 1.205) suggest that *A. lituratus* is the most important disperser species, followed by *C. perspicillata* (DII = 1.049) and *U. bilobatum* (DII = 0.023). Likewise, for the urban area, *A. lituratus* (DII = 0.530) is the most important disperser species, followed by *C. perspicillata* (DII = 0.212) and *U. bilobatum* (DII = 0.026; Table 3).

Discussion

The present research assessed how the areas with urban growth that maintain relicts of TDF have affected the species composition and diversity for different bat guilds and the composition of the food resources for the family Phyllostomidae. Our results support this hypothesis by showing a marked difference in bat species richness and abundance between the urban (112 individuals, seven species) and peri-urban (164 individuals, ten species) TDF areas. In the urban area, we observed a notable reduction in species richness and total bat abundance compared to the peri-urban area. This discrepancy may be linked to habitat size and structure (Garcés-Restrepo *et al.* 2016; Chacón-Pacheco *et al.* 2017) since the peri-urban area maintains greater continuity in its floristic composition and a lower degree of alteration due to human activity. In addition, the importance of natural corridors between forest fragments

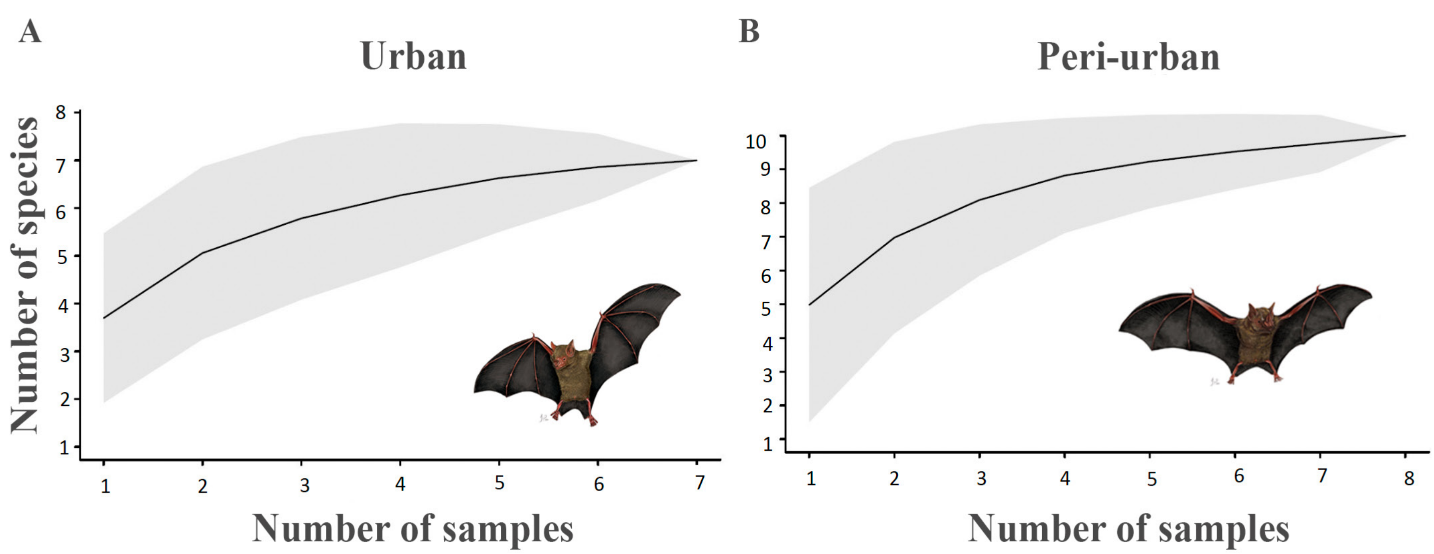

Figure 4. Rarefaction curve of the bat assemblage in the study areas.

Table 2. Percentage of occurrence (PO) of fruit species consumed by bats inhabiting urban and peri-urban TDF fragments.

Fragments	Bat species	Fruit species						
		Cecropia sp.	*F. obtusifolia*	*P. aduncum*	*P. guajava*	*S. lycopersicum*	*M. indica**	*M. zapota**
Urban	*A. lituratus*	20.0	40.0	30.0	30.0	0	25.0	0
	C. perspicillata	50.0	55.6	22.2	22.2	0	1.7	0
	G. soricina	33.3	0	66.7	0	0	0	0
	S. lilium	0	50.0	100.0	0	0	0	0
	U. bilobatum	33.3	50.0	33.3	33.3	0	0	0
Peri-urban	*A. lituratus*	40.6	50.0	25.0	21.8	25.0	21.8	43.7
	C. perspicillata	19.4	33.3	30.6	13.9	41.7	0	0
	G. soricina	33.3	33.3	66.7	0	0	0	0
	S. lilium	0	33.3	33.3	0	33.3	0	0
	U. bilobatum	40.0	80.0	40.0	0	0	0	0
	C. brevicauda	0	25.0	0	25.0	75.0	0	0
	P. fusciventris	0	66.7	33.3	0	33.3	0	0

* Direct field observations

is worth highlighting, as these favor the dynamics and stability of animal communities in urbanized areas (Gehrt and Chelsvig 2004; Hale *et al.* 2012). Our results are consistent with previous studies indicating a decrease in bat richness in urban areas and suggest that species of the family Phyllostomidae, with their generalist adaptability, play a central role in the colonization of disturbed habitats (Quinto-Mosquera *et al.* 2013). Taken together, these findings underline the relevance of considering the effects of habitat reduction on the conservation of bat diversity in urbanized landscapes and emphasize the need to implement strategies that promote the connectivity between habitats to preserve the local fauna (Hahs *et al.* 2023).

The 11 species of bats recorded in the Cúcuta urban and peri-urban areas account for 5.33 % of the species known for Colombia. In turn, the diversity reported in this work agrees with similar figures reported for other TDF ecosystems. For example, Sánchez *et al.* (2007) reported 12 species in Chicamocha and Patia. Cabrera et al. (2016) found nine species in three dry ecosystems transformed by crops in Nariño. For their part, Vela-Vargas and Pérez-Torres (2012) reported 20 species in a livestock area in the department of Cordoba. However, this variation in richness is generally associated with habitat deterioration (Ortega and Mantilla-Meluk 2008). This can be represented by high abundance records of common species (*e. g.*, *U. bilobatum*, *C. perspicillata,* and *S. lilium*).

Diet composition of phyllostomid bats. Nine species of the family Phyllostomidae were recorded (Table 1), corresponding to 9 % of the total phyllostomid species recorded for Colombia, where the most abundant species are *A. lituratus* and *C. perspicillata*. The richness observed in the urban and peri-urban areas is consistent with the results repored by Aroca *et al.* (2016) in dry forest patches in the Department of Caldas, where eight frugivorous bat species were recorded, with a higher relative abundance of *C. perspicillata*, followed by *U. bilobatum* and *A. lituratus*. The studies by Ríos-Blanco and Pérez-Torres (2015) in a native TDF fragment in the municipality of Buenavista, Cordoba, recorded 17 phyllostomid species, coinciding with our study in that the most abundant species were *A. lituratus*, *C. perspicillata,* and *U. bilobatum*.

Our study on the diet of urban and peri-urban bats identified a recurrent presence of plants belonging to the genera *Piper*, *Cecropia*, *Ficus,* and *Solanum*. On the other hand, the genera *Manilkara*, *Psidium,* and *Mangifera* were less represented. Although it has been documented that Neotropical frugivorous bats show a preference for species of the genera *Ficus* and *Solanum* (Muscarella and Fleming 2007; Estrada-Villegas *et al.* 2010; Suárez-Castro and Montenegro 2015; Anteliz-Pallares *et al.* 2021; Velásquez-Roa *et al.* 2023), our study highlighted a particular trend: these bats demonstrate a marked preference for domesticated species, especially those from crops, plantations, or orchards near TDF patches (refer to Figure 1, crop mosaics). Such a preference may influence seed dispersal, potentially favor-

Table 3. Percent values of captures, samples containing seeds, and disperser index (DII) for each frugivorous bat species inhabiting the urban and peri-urban communities.

Fragments	Bat species	Percentage of catches	Samples with seeds	DII
Urban	*A. lituratus*	54.1	9.80	0.530
	C. perspicillata	24.1	8.82	0.212
	U. bilobatum	9.1	2.94	0.026
	G. sorcsina	5.5	1.47	0.008
	S. lilium	2.7	0.98	0.002
	A. obscurus	0	0	0
Peri-urban	*A. lituratus*	43.8	27.52	1.205
	C. perspicillata	33.9	30.96	1.049
	U. bilobatum	5.5	4.30	0.023
	C. brevicauda	4.3	3.44	0.014
	P. fusciventris	4.3	2.58	0.011
	G. soricina	3.7	2.58	0.009
	S. lilium	1.8	2.58	0.004
	D. roduntus	0	0	0
	P. parnellii fusco	0	0	0

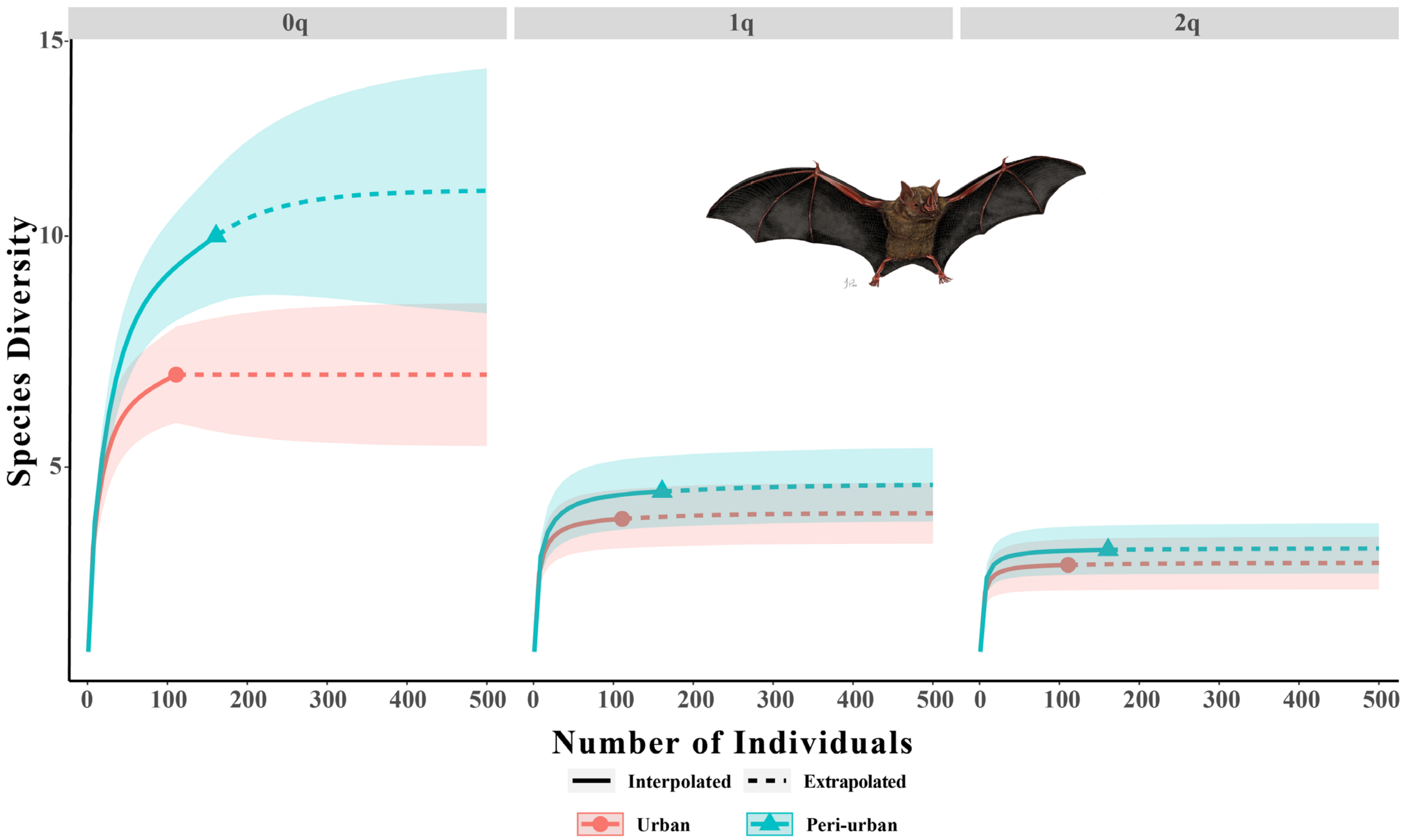

Figure 5. Diversity profiles of bats in the urban and peri-urban TDF fragments in the Cúcuta metropolitan area. Diversity orders: ^{0}q; ^{1}q; ^{2}q.

ing these domesticated species at the expense of wild ones. This relationship between bats and domesticated plants emphasizes the importance of further investigating its effect on the structure and composition of the TDF, as well as its role in the natural regeneration processes in central and peripheral zones of the Cúcuta metropolitan area.

However, two plant records, *Cecropia* sp. and *P. aduncum*, are characteristic of the TDF. In particular, *Cecropia* sp. was found in four of five bat species in urban areas and four of seven species in peri-urban zones. For its part, the shrub *P. aduncum* (family Piperaceae) was detected in the feces of all urban and six peri-urban bat species (Table 2). Given its ability to colonize perturbed areas, this plant probably plays a role as a pioneer or early-succession plant in dry forests, rapidly establishing in open or altered zones. These characteristics favor colonization by other species since environmental conditions are modified, either by enriching the soil or providing shade (Fleming 2004). Interestingly, mid-sized to large species, such as *S. lilium* (total length of 62 to 65 mm; forearm 36.6 to 45.0 mm; Gannon *et al.* 1989), showed a less varied diet in urban and peri-urban zones, as detailed in Table 2. However, they showed 100 % occurrence (PO) for *P. aduncum*. This affinity may involve significant consequences because fruit dispersal by bats may boost regeneration in perturbed zones within urban and peri-urban areas, in agreement with the ecological role proposed for *Piper* in dispersal and ecological succession (Fleming 2004). In this regard, Muscarella and Fleming (2007) state that Neotropical frugivorous phyllostomid bats are essential in the early forest succession stages, given the importance of fruits of early-succession shrubs and trees in their diet. These phyllostomid bats are vital facilitators of early forest regeneration, indirectly boosting the incorporation of plant species characteristic of TDFs. Besides, some reports mention that *S. lilium* feeds mainly on fruits of the families Solanaceae, Piperaceae, and Moraceae (Calonge 2009), emphasizing its key role in the regeneration process in TDF patches.

Separately, *C. brevicauda* is a mid-sized species (forearm 36 to 43 mm; mid-sized tibia 16 to 20 mm) that thrives in the low forest stratum that concentrates most shrubs and plants that produce the seeds it consumes (Emmons and Feer 1999). For *C. brevicauda*, this study recorded that it consumes three types of fruits in the peri-urban area, *Solanum* being the most frequent in the diet (75 %), followed by *Ficus* and *Psidium* (25 %). These findings contrast with those of Estrada-Villegas *et al.* (2010), who recorded that *C. brevicauda* consumed mostly fruits of the family Piperaceae and, to a lesser extent, of the family Solanaceae. However, *C. brevicauda* is able to exploit a broad range of food resources according to fruit availability and abundance in the areas where it lives (Aroca *et al.* 2016; Anteliz-Pallares *et al.* 2021), as well as to the degree of alteration and, hence, the vegetation structure and composition in these zones relative to the study area. On the other hand, *Platyrrhinus fusciventris* consumed fruits from three genera of plants in the peri-urban area, *Ficus* being the most frequent (66.6 %), followed by *Piper* and *Solanum* (33.3 %). Our findings are consistent with other studies that reported a preference for the genera *Solanum, Piper,* and *Ficus* by *Platyrrhinus* spp. (Aroca *et al.* 2016).

Likewise, other studies report that *Artibeus* spp. feed mainly on *Ficus* spp. (Gardner 2008), similar to the findings in the present study (Thies and Kalko 2004) in urban and peri-urban areas. However, Gorchov *et al.* (1995) found a larger number of *Cecropia* seeds in the feces of *Artibeus* spp. than in other species. Also, *C. perspicillata* showed a diet including fruits of the genus *Ficus*, with 41.6 % for the peri-urban zone and 55.5 % for the urban area. This finding contrasts with the reports for *Carollia* spp., where the main food sources are plants of the genera *Solanum* and *Piper* (Giannini and Kalko 2004). The feeding patterns of some bat species in TDFs may be influenced by limited food availability, particularly in the fragments studied, given the degree of alteration, in contrast with other tropical forests (Apgaua *et al.* 2014). Regarding the diversity of plant families in the TDF, Suárez *et al.* (2004) reported that *Machaerium* sp. (Fabaceae) showed the highest density, with 12.20 %, followed by *Croton cucutencis* and *C.* aff. *croizatti* (Euphorbiaceae), with densities of 11.08 % and 10.70 %, respectively. Despite that García-Herrera *et al.* (2019) documented the interaction of bats with plants of these families, our study did not show the presence of plants with the highest density in the TDF in the diet of bats. It is worth highlighting that although the families Asteraceae and Euphorbiaceae are dominant in TDFs, it is vital to understand the relationship between the abundance of these plants and the consumption of their fruits by bats. This interaction becomes even more relevant considering the expansion of crops and orchards, which have increased the presence of domestic plants.

The findings of the present study indicate that *A. lituratus* is one of the most important disperser bat species in urban and peri-urban areas, so it might greatly influence the restoration of areas perturbed by agriculture and livestock raising, as was the case of the areas assessed in this study. Hahs *et al.* (2023) found that bats in urban zones show traits typical of mobile generalists, favored by urbanization in species with strong dispersal abilities, versatile diets, and reproductive strategies that allow them to use the available resources efficiently. Novoa *et al.* (2011) reported a similar pattern in a dry forest, where the genera *Artibeus* and *Carollia* were also the main dispersers within the bat assemblage. According to the Disperser Importance Index (Table 3), all species in the urban and peri-urban areas showed lower values than those reported by Galindo-González *et al.* (2000) but were similar to those reported by Ríos-Blanco (2015). This may be due mainly to the number of samples collected: when the number of samples per species is low, this index probably underestimates the importance of the disperser; therefore, a greater sampling effort is needed to collect a larger number of samples. Previous works applying the disperser importance index (Galindo-González *et al.* 2000; Loayza *et al.* 2006) reveal that the highest value generally corresponds to the most abundant species that attain the largest number of samples analyzed, consistent with our findings in the present study.

This research shows that bats inhabiting urban and peri-urban areas preferentially consume fruits of domesticated plant species. In the urban landscape, the fruits consumed preferentially by bats are those of *F. obtusifolia* (fig) and *P. guajava* (guava), although native species, such as *P. aduncum* and *Cecropia* sp., are also included in the diet of all the bat species collected. In the peri-urban environment, we observed an even more pronounced preference for fruits of domesticated species, particularly fruits of high economic importance such as *P. guajava, S. lycopersicum* (tomato), *F. obtusifolia, M. zapota* (zapote), and *M. indica* (mango). These results suggest that in peri-urban areas, the food preference of bats may be shifting from wild species to domesticated and cultivated plants. Our findings underline the need to carry out further in-depth studies to understand the impact of this shift in the diet on seed dispersal and ecological dynamics in the study areas.

Acknowledgments

The authors wish to thank the Biology department, the Research Vice-Rectory, and the Ecology and Biogeography Research Group (GIEB) at Universidad de Pamplona for their support and assistance during field trips. We are particularly grateful to HECASA and its director, L. R. Sánchez, for assisting in the identification of plant specimens. Thanks also to the Museo de Ciencias Naturales J. Celestino Mutis (Museum of Natural Sciences) staff and its director, J. Sierra, for the support in processing and identifying bat specimens. To O. Armesto, H. Cristancho, and L. F. Galeano for their logistics and field assistance. To J. A. Pabón for the figures. To IdeaWild for providing free equipment. Special thanks to the officers of Ecoparque Comfanorte de Cúcuta for their interest in the ecology and biodiversity conservation projects for Cúcuta and for facilitating the field sampling. M. E. Sánchez-Salazar translated the manuscript into English.

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Associated editor: Cintya A. Segura Trujillo
Submitted: June 15, 2023; Reviewed: July 6, 2023
Accepted: September 15, 2023; Published on line: September 26, 2023