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Diet of frugivorous bats and resource availability in a tropical dry forest of Northeastern Colombia

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Tropical dry forests are among the most transformed and threatened ecosystems in Colombia, where habitat fragmentation can alter resource availability and ecological interactions between plants and frugivorous bats. We evaluated the diet of frugivorous bats and its relationship with plant resource availability in a heterogeneous tropical dry forest landscape. Bats were sampled with mist nets across different vegetation cover types, including tropical dry forest remnants, pastures, and transition zones. Vegetation was characterized using sampling plots. Dietary interactions were documented primarily by identifying seeds present in fecal samples; two additional bat-plant links were documented through direct observations of fruit feeding. These records were used to build a bat-plant network describing the structure of trophic interactions. The network included seven bat taxa with records of fruit consumption, and interactions were concentrated on *Artibeus planirostris* and *Sturnira tildae*. The vegetation was composed largely of plant species typical of disturbed habitats and agricultural matrices. The interaction network had a connectance of 0.33 and specialization of $H_2' = 0.38$, with most interactions concentrated among generalist taxa. The most frequently recorded dietary resources were *Piper* sp., *Cissus* sp., and *Muntingia calabura*, highlighting their importance in the landscape. Several of these frequently recorded dietary resources were not detected in the vegetation plots, indicating that bats exploited food resources beyond the vegetation sampling units. Our results highlight the potential ecological role of frugivorous bats in fragmented tropical dry forest landscapes, where they may contribute to seed dispersal and vegetation regeneration despite substantial anthropogenic transformation.

Keywords: interaction networks, landscape fragmentation, resource availability, seed dispersal.

Los bosques secos tropicales están entre los ecosistemas más transformados y amenazados de Colombia, donde la fragmentación puede modificar la disponibilidad de recursos y las interacciones ecológicas entre plantas y murciélagos frugívoros. Evaluamos la dieta de murciélagos frugívoros y su relación con la disponibilidad de recursos vegetales en un paisaje heterogéneo de bosque seco tropical. Los murciélagos se muestrearon con redes de niebla en remanentes de bosque seco, pastizales y zonas de transición; la vegetación se caracterizó mediante parcelas. La dieta se documentó principalmente con semillas de muestras fecales; dos enlaces adicionales procedieron de observaciones directas de alimentación. Con estos datos construimos la red murciélago-planta. La red incluyó siete taxones de murciélagos con registros dietarios de consumo de frutos, y las interacciones se concentraron principalmente en *Artibeus planirostris* y *Sturnira tildae*. La composición vegetal estuvo representada sobre todo por especies típicas de ambientes intervenidos y matrices agropecuarias. La red de interacción presentó una conectancia de 0.33 y una especialización de $H_2' = 0.38$, con la mayoría de las interacciones concentradas en taxones generalistas. Los recursos dietarios registrados con mayor frecuencia fueron *Piper* sp., *Cissus* sp. y *Muntingia calabura*, evidenciando su importancia como recursos alimenticios dentro del paisaje. Varios de los recursos dietarios registrados con mayor frecuencia no fueron detectados en las parcelas de vegetación, lo que indica que los murciélagos explotaron recursos alimenticios fuera de las unidades de muestreo de vegetación. Los murciélagos frugívoros pueden contribuir a la dispersión de semillas y a la regeneración vegetal incluso en paisajes secos fragmentados y transformados.

Palabras clave: dispersión de semillas, disponibilidad de recursos, fragmentación del paisaje, redes de interacción.

In Colombia, tropical dry forests (TDFs) occur across six biogeographic regions, including the Caribbean region, the inter-Andean valleys of the Cauca and Magdalena rivers, the northern Andean region of Santander and Norte de Santander, the Patía River valley, and rocky outcrops in Arauca and Vichada within the Orinoco lowlands (Pizano *et al.* 2017). The Caribbean region contains approximately 40% of these dry ecosystems, which are complex natural systems whose ecological dynamics are shaped by interactions among climatic variation, edaphic conditions, and different degrees of anthropogenic disturbance (Pizano *et al.* 2017; Ministerio de Ambiente y Desarrollo Sostenible 2020). According to the Holdridge life-zone classification, TDFs are vegetation formations characterized by relatively continuous forest cover, temperatures above 24 °C, annual rainfall that may reach 2,000 mm, well-defined wet and dry seasons, and an elevational distribution from 0 to 1,000 m.a.s.l. (Holdridge 1987; Pizano *et al.* 2016).

Tropical dry forests provide ecosystem services that emerge from interactions between biotic and abiotic components and can be interpreted according to their ecological, social, cultural, or economic value (de Groot *et al.* 2002; Anaya Cristancho 2015). These services are particularly important for human communities and include hydrological regulation, soil retention, carbon sequestration, and the availability of water and nutrients (Pizano *et al.* 2017). In addition to these regulating services, TDFs also provide provisioning resources, including fruit-producing plant species that serve as food for wildlife and local communities and therefore have socioeconomic relevance (Ministerio de Ambiente y Desarrollo Sostenible 2020).

From a floristic perspective, Colombian TDFs include approximately 2,600 recorded plant species, reflecting the structural and functional complexity of this ecosystem (Pizano *et al.* 2016). Within this flora, several species produce fruits that are important food resources for various groups of wildlife, promoting multiple ecological interactions and contributing to the maintenance of trophic networks (Devia *et al.* 2014).

This ecosystem is among the most threatened in Colombia, with the loss of more than 90% of the original cover due to agricultural and livestock expansion, infrastructure development, mining, and intensive logging, all of which have transformed the landscape and degraded soils (López *et al.* 2019; Gómez-Pacheco *et al.* 2025). These anthropogenic pressures have subdivided formerly continuous habitats into multiple patches separated by human-modified matrices, producing landscapes that are more heterogeneous and functionally less connected (García 2011; Herrera 2011; Valdés 2011). In this context, vegetation patches function as habitat remnants whose ecological value is determined by their size and resource availability (González-Caro and Vásquez 2018). Plant-animal interactions are also directly affected by reductions in floristic diversity and fragment integrity (Loayza *et al.* 2006).

Due to the strong seasonality of rainfall and high environmental heterogeneity in TDFs, resource availability directly shapes the spatial distribution and diet of the fauna (Rojas Murcia *et al.* 2016). These conditions affect plant establishment patterns and structural attributes of the forest, particularly leaf cover (de Oliveira e Silva *et al.* 2017; Siyum 2020). Seasonal variation in resource availability can also influence reproductive, social, and territorial behavior in animals (Wallace and Painter 2003). During the dry season, reduced rainfall changes forest physiognomy and decreases primary productivity and food availability for fauna, which is reflected in lower biological activity within the ecosystem (Martínez-Hernández *et al.* 2019).

Natural regeneration and restoration processes in disturbed areas are strongly mediated by mechanisms such as seed dispersal (Dániel Ferreira 2009). Frugivorous animals act as effective seed dispersers in forests, and bats stand out as primary agents because of their high diversity, mobility, nocturnal behavior, and ecological adaptations (Galindo-González 1998; Kattán 2003; Parrado-Rosselli 2007).

Colombia is one of the richest countries in the Neotropics in terms of bat diversity, with approximately 220 recorded species (Díaz *et al.* 2021; Pabón *et al.* 2023). Seed-dispersing bats mainly belong to the family Phyllostomidae, which is recognized by the presence of a characteristic cutaneous structure, the noseleaf, located at the anterior end of the nose, which contributes to the emission and direction of echolocation calls during foraging (Galindo-González 1998). This family is highly diverse and often dominant in both species richness and abundance (García-García and Santos-Moreno 2014). The diet of frugivorous bats is diverse and flexible, allowing them to adapt to different environments and temporal variation in resource availability. Although many species tend to rely on key fruit resources, they may also incorporate a broad range of plant species depending on their temporal supply in the forest (Loayza *et al.* 2006). In addition, several predominantly frugivorous bat species may complement their diet with insects, particularly during periods of low fruit availability, such as the dry season (Lenoble *et al.* 2014; Ingala *et al.* 2021).

Resource selection by frugivorous bats does not depend only on fruit availability, but also on nutritional properties such as sugar, lipid, and water content, all of which influence feeding decisions (Galindo-González 1998). Species may also switch among fruit resources depending on their physiological requirements and the reproductive or energetic condition of individuals (Estrada-Villegas *et al.* 2007).

In fragmented TDF landscapes, the availability and spatial distribution of plant species can influence interactions between plants and fruit-feeding bats. We therefore characterized the plant resources recorded in vegetation plots and the diet of bats to evaluate their correspondence within the study landscape. Because bats are highly mobile, we expected dietary records to include both plant resources detected locally in the vegetation plots and those not recorded within them. This descriptive framework identifies key plant resources and clarifies the potential role of bats as seed dispersers without inferring resource selection or proportional use from the available data.

Materials and methods

Study area. The study was conducted in Puerto Mosquito, a rural district in the Municipality of Gamarra, southern Cesar Department, Colombia. The study site is located approximately at 8.19° N, 73.76° W, at 50 to 60 m.a.s.l. (Municipio de Gamarra 2012). Its geographical location is shown in Figure 1. The Municipality of Gamarra lies in the Magdalena River valley within the warm thermal belt, with elevations between 0 and 100 m.a.s.l. and temperatures above 24 °C. The mean annual temperature is approximately 28.4 °C, with an average relative humidity of 78% (Municipio de Gamarra 2012). The study area is part of the tropical dry forest region, representing one of the main distribution centers of this ecosystem in the Magdalena River valley.

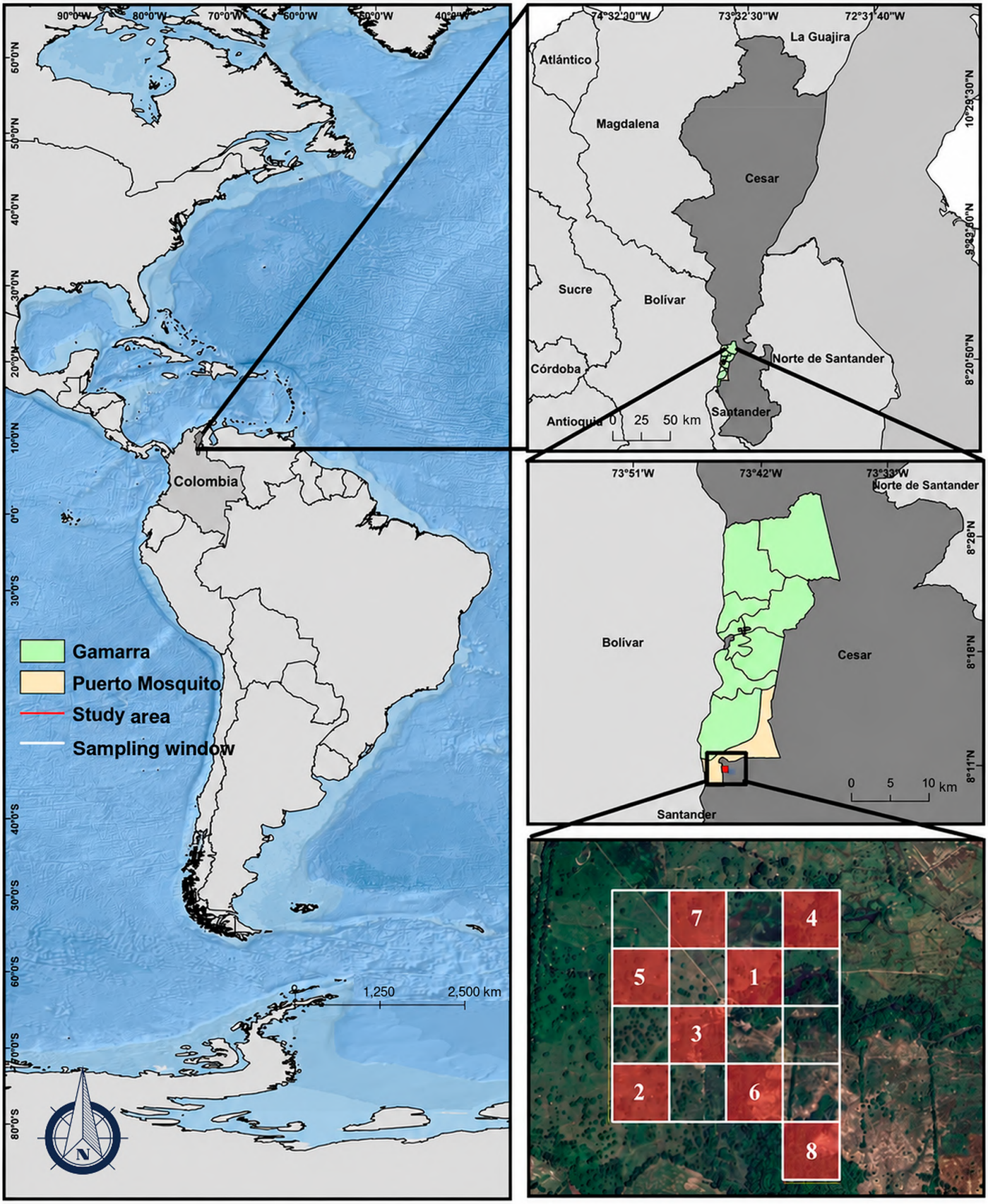

Figure 1. Location of the study area in Puerto Mosquito, Municipality of Gamarra, Cesar Department, Colombia, showing the 700 × 700 m sampling window and the eight selected 175 × 175 m sampling cells.

The current landscape is highly transformed, with remnants of natural vegetation embedded in an agricultural and livestock matrix (Municipio de Gamarra 2012).

Selection of sampling cells. Sampling was conducted within a 700 × 700 m sampling window (Figure 1), which was divided into sixteen 175 × 175 m sampling cells, following

the approach proposed by Colorado-Zuluaga *et al.* (2017). The cells were distributed across different landscape units, including forest fragments that differed in connectivity and successional stage. Potential sampling cells were identified through satellite image analysis and preliminary field surveys. Fragments were classified according to vegetation cover type, degree of isolation, and successional condition. From the sixteen available cells, eight were selected using an interspersed random design for sampling. One selected cell was slightly displaced relative to the initial grid to include a forest patch with greater vegetation cover while maintaining the criteria of landscape representativeness.

Bat assemblage sampling. Bat captures were conducted during two field campaigns between January and April 2026. The first campaign was carried out from January 29 to February 22, 2026, comprising two sampling nights per cell across eight sampling cells (16 sampling nights). This period coincided with a climatic transition characterized by alternating dry conditions and episodic rainfall. The second campaign was conducted from March 28 to April 7, 2026, under dry-season conditions, and consisted of one sampling night per cell (8 sampling nights). To characterize the bat assemblage, all captured individuals were included in the general inventory. However, network and diet analyses were restricted to taxa with documented fruit consumption, either from fecal samples or direct feeding observations, regardless of their primary trophic-guild classification. Sampling cells were distributed across the fragmented landscape, including forest remnants and pastures, thereby incorporating environmental and land-use heterogeneity into the ecological analyses. The two campaigns were not treated as replicated seasons because each climatic period was represented by a single campaign and sampling effort differed between them (16 *vs.* 8 nights); therefore, campaign and climatic period were confounded.

Each night, three mist nets measuring 12 × 2.5 m were installed along strategic flight corridors, including the understory, forest edges, and areas near potential roosts. Mist nets remained open from 18:00 to 00:00 h, a period that overlaps with high bat activity. To reduce stress in captured individuals, mist nets were checked every 15 min (Giraldo *et al.* 2011; Pabón *et al.* 2023; Velásquez Roa *et al.* 2023).

Captured bats were identified to the lowest reliable taxonomic level using updated taxonomic keys (Díaz *et al.* 2021). For each individual, we recorded sex, reproductive condition (pregnancy, lactation, or descended testes), relative age (juvenile or adult, based on the degree of ossification of the wing epiphyseal joints) and morphometric measurements including total length, forearm length, hind foot length, ear length, noseleaf length, and tail length (Giraldo *et al.* 2011; Anteliz-Pallares *et al.* 2021). To identify recaptures and evaluate space-use patterns, bats were marked with combinations of colored nail polish applied to the claws according to a sampling-unit-specific code. This non-invasive technique allowed individual recognition and the detection of movements among sampling cells within the landscape (Rodríguez-Posada and Santa-Sepúlveda 2013).

To support taxonomic identification, some individuals were collected as reference specimens following ethical protocols (Supplementary data SD1). These specimens were prepared and deposited in the mammal collection of the Museo de Ciencias Naturales José Celestino Mutis, Universidad de Pamplona, following Simmons and Muñoz-Saba (2005). Collections were conducted under the collection permit issued by the Autoridad Nacional de Licencias Ambientales (ANLA), Resolution No. 002382 of 30 October 2025.

Plant resource availability. To characterize the flora of the study area, vegetation was sampled using plots established in each selected sampling cell. Four 20 × 20 m plots were established in each sampling cell, located in the most floristically representative sites. Within each plot, all plant individuals with diameters greater than 2.5 cm were recorded. For each individual, we recorded height, foliage cover, diameter, and the observed percentage of flowering and fruiting at the time of sampling (Ruiz-V and Saab-R 2020; Mora-Yela *et al.* 2025). Because fruit biomass was not quantified, vegetation data were interpreted as an index of locally recorded plant-resource availability rather than as a direct quantitative estimate of fruit supply.

When possible, one voucher specimen per taxon was collected, preferably with reproductive structures (Supplementary data SD2). Specimens were transported to the Herbario Catatumbo Sarare (HECASA) for identification through comparison with reference material and consultation of virtual herbaria. Collection of botanical reference material was conducted under the collection permit issued by ANLA, Resolution No. 002382 of 30 October 2025. We reviewed the literature on plant taxa reported as food resources for bats in tropical dry forests. Plant taxa with published evidence of bat consumption were classified as potential food resources, whereas taxa for which no such evidence was found in the reviewed literature were classified as other recorded plant taxa. This literature-based classification was used only to group the plant taxa recorded in the vegetation plots and was independent of the dietary evidence used to establish the bat–plant interactions described below.

Diet. Captured bats were kept temporarily in cloth bags for approximately 60 min to allow fecal sample collection. Fecal samples were preserved in Eppendorf tubes with 70% ethanol for subsequent analysis (Pabón *et al.* 2023; Velásquez Roa *et al.* 2023). After fieldwork, fecal samples were transported to the laboratory, washed with water, and examined under a stereoscope to identify seeds. Seed identification was performed by comparison with fruits collected in the study area and using the guide by Oliveira and Pereira (2016) and the online Seed Identification Guide (2026) (Supplementary data SD2). The bat-plant network was based primarily on dietary records that could be reliably assigned to a plant taxon from fecal material; unidentifiable

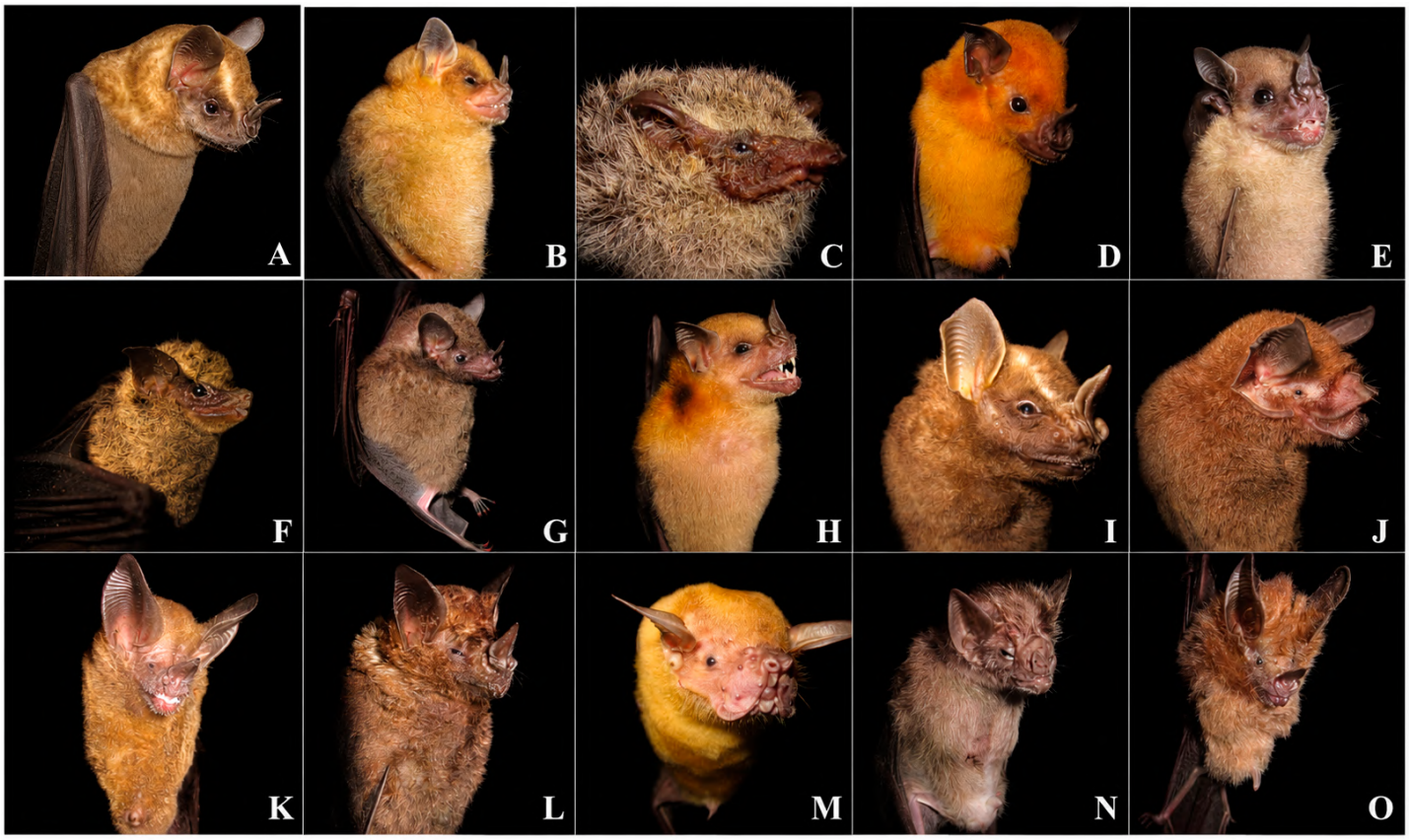

Figure 2. Photographic plate of bat taxa recorded in the tropical dry forest of Puerto Mosquito, Cesar, Colombia. A. *Artibeus planirostris.* B. *Sturnira tildae.* C. *Rhynchonycteris naso.* D. *Phyllostomus discolor.* E. *Sturnira giannae.* F. *Saccopteryx canescens.* G. *Glossophaga soricina.* H. *Sturnira* sp. I. *Artibeus lituratus.* J. *Pteronotus* sp. K. *Trachops cirrhosus*. L. *Carollia perspicillata*. M. *Noctilio leporinus*. N. *Desmodus rotundus*. O. *Micronycteris microtis*.

Table 1. Composition and abundance of bat taxa recorded in the tropical dry forest of Puerto Mosquito, Cesar, Colombia.

Family	Taxon	Trophic guild	Abundance	Relative frequency (%)
Phyllostomidae	*Artibeus planirostris* (Figure 2A)	Frugivore	63	33.87
	Phyllostomus discolor (Figure 2D)	Omnivore	23	12.37
	Sturnira tildae (Figure 2B)	Frugivore	23	12.37
	Sturnira giannae (Figure 2E)	Frugivore	13	6.99
	Glossophaga soricina (Figure 2G)	Nectarivore	10	5.38
	Sturnira sp. (Figure 2H)	Frugivore	8	4.30
	Artibeus lituratus (Figure 2I)	Frugivore	3	1.61
	Carollia perspicillata (Figure 2L)	Frugivore	2	1.08
	Trachops cirrhosus (Figure 2K)	Carnivore	2	1.08
	Desmodus rotundus (Figure 2N)	Sanguivore	1	0.54
	Micronycteris microtis (Figure 2O)	Insectivore	1	0.54
Emballonuridae	*Rhynchonycteris naso* (Figure 2C)	Insectivore	23	12.37
	Saccopteryx canescens (Figure 2F)	Insectivore	10	5.38
Mormoopidae	*Pteronotus* sp. (Figure 2J)	Insectivore	3	1.61
Noctilionidae	*Noctilio leporinus* (Figure 2M)	Piscivore	1	0.54

material was excluded from network analyses. In addition, direct field observations of bats feeding on fruits of *Mangifera indica* and *Manilkara zapota* were used to document those specific interactions. These observations were included as evidence of fruit consumption, but not of seed ingestion or dispersal.

Data analysis. Sampling completeness was evaluated using the sample coverage estimator, which estimates the proportion of the total assemblage represented in the sample based on the frequency of rare taxa. This analysis was performed using the iNEXT package in RStudio (Hsieh *et al.* 2016; R Core Team 2024; Posit team 2026). Diversity of the bat and plant assemblages was evaluated using Hill numbers. For both groups, diversity was estimated at three orders: q_0, taxon richness; q_1, exponential Shannon diversity, which weights common taxa; and q_2, inverse Simpson diversity, which emphasizes dominant species (Chao *et al.* 2014).

To describe assemblage structure, rank-abundance

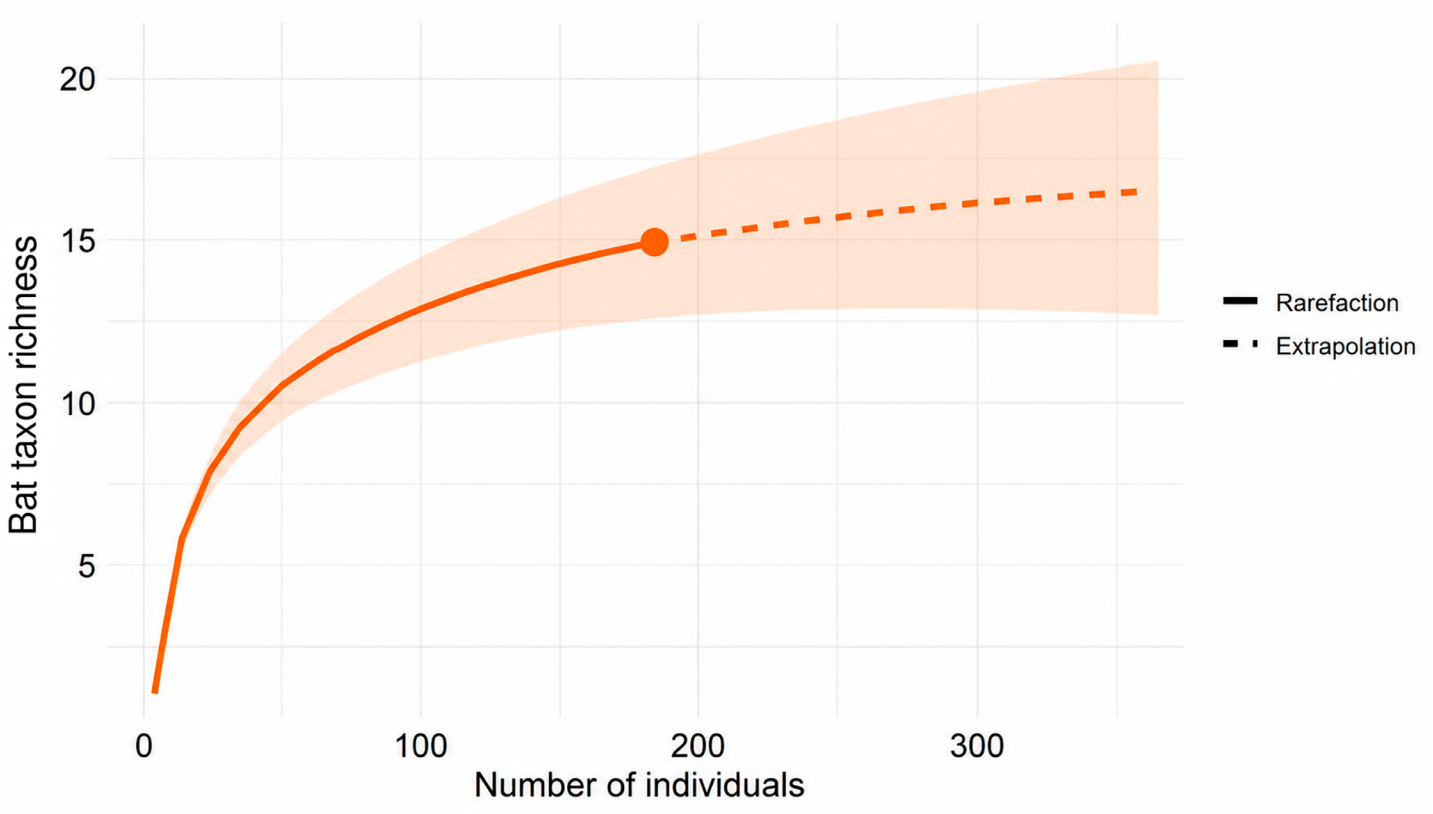

Figure 3. Sample-size-based rarefaction (solid line) and extrapolation (dashed line) of bat taxon richness (q_0) as a function of the number of individuals. The filled circle marks the observed reference sample (186 individuals, 15 taxa), and the shaded area represents the 95% confidence interval.

curves were constructed to visualize dominance and evenness within each assemblage (Santos-Andrade 2023). For the plant assemblage, separate rank-abundance curves distinguished potential bat food resources, based on the literature review described above, from other recorded plant taxa. Plant diversity was analyzed at the plot scale (n = 32) to capture spatial variation within the study area. Descriptive measures of Hill numbers, including mean, range, and distribution, were calculated to evaluate heterogeneity patterns in the plant assemblage. Beta diversity was evaluated using dissimilarity analyses based on the Jaccard index, which considers taxon presence and absence among sampling units. From this dissimilarity matrix, a hierarchical clustering dendrogram was built to identify patterns of floristic similarity among plots. These analyses were performed with functions from the vegan package in R (Núñez-Colín and Escobedo-López 2011; R Core Team 2024; Posit team 2026).

For bat-plant interactions involving taxa with dietary evidence of fruit consumption, network metrics were calculated to describe the structure of ecological interactions, including connectance, link density, links per taxon, nestedness, and network specialization (H2′). Taxon-level specialization was estimated using the d′ index and degree, or number of interactions, to identify generalist and specialist taxa within the network (Mora and Dáttilo 2021). For bat taxa with the fecal-sample information required for the calculation, disperser importance was evaluated using the Disperser Importance Index (DII; Galindo-González *et al.* 2000), calculated from relative abundance and the percentage of fecal samples containing seeds. Direct feeding observations were not used to infer seed dispersal and were excluded from the DII calculation. Interaction networks and ecological metrics were analyzed and visualized in R version 4.4.1, mainly using the bipartite, igraph, ggraph, and ggplot2 packages (R Core Team 2024; Posit team 2026).

Ethics statement. Bat capture, handling, collection, and release were conducted following the guidelines for the use of wild mammals in research proposed by Sikes *et al.* (2016), ensuring animal welfare and minimizing stress during sampling. The study was conducted under the collection permit issued by ANLA, Resolution No. 002382 of 30 October 2025.

Results

Bat taxon composition. We recorded 186 individuals distributed among four families, 12 genera, and 15 operational taxa, of which 13 were identified to species and two to genus (Figure 2; Table 1). Sampling effort was 5,184 m-net-h, calculated as the product of the number of mist nets, mist net length, nightly opening time, and number of sampling nights, following Bogdanowicz *et al.* (2009). Sampling completeness was 98.4% (Figure 3), indicating adequate sampling to characterize the bat assemblage.

Hill numbers showed a difference between observed richness and effective diversity. We recorded 15 taxa (q_0 = 15), whereas diversity of order 1 (q_1 = 8.11) indicated that

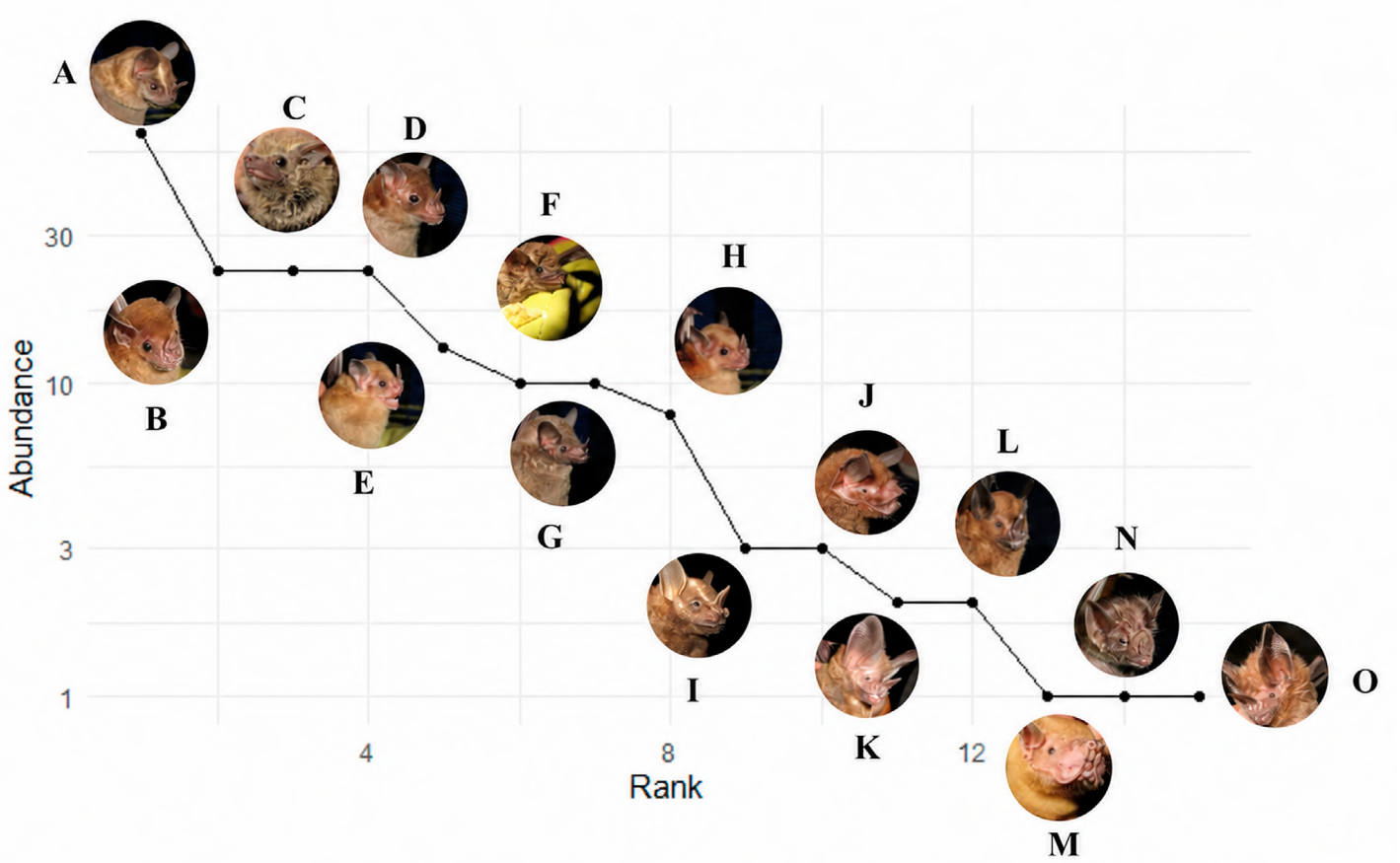

Figure 4. Rank-abundance curve of bat taxa recorded in the tropical dry forest of the study area. Letters A-O correspond to the taxa shown in Figure 2 in the same order.

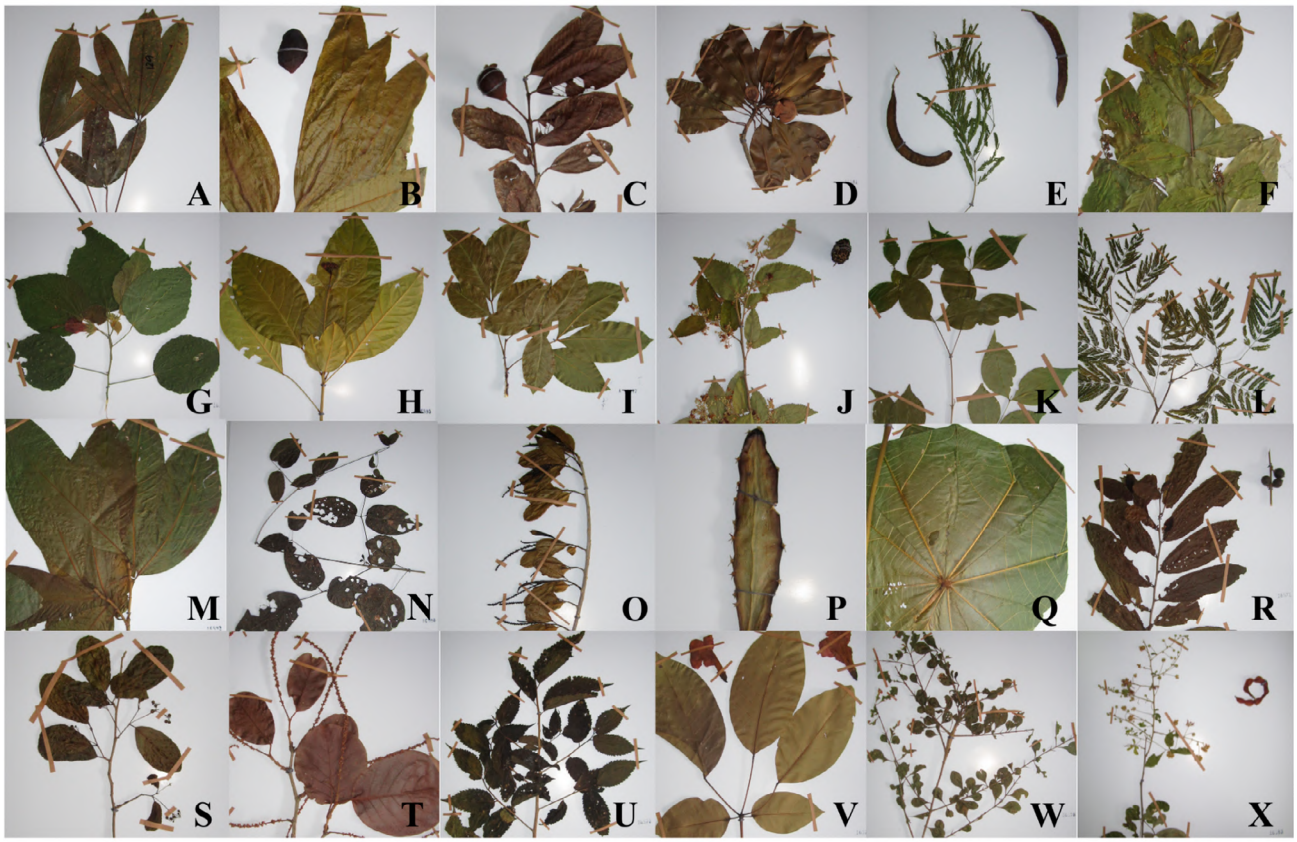

Figure 5. Photographic plate of plant taxa recorded in the tropical dry forest of Puerto Mosquito, Cesar, Colombia. A. *Ceiba pentandra*. B. *Mangifera indica*. C. *Psidium guajava*. D. *Manilkara zapota*. E. *Chloroleucon mangense*. F. *Bunchosia hartwegiana*. G. *Malvaviscus arboreus*. H. *Morisonia americana*. I. *Melicoccus bijugatus*. J. *Guazuma ulmifolia*. K. *Malpighia glabra*. L. *Enterolobium cyclocarpum*. M. *Triplaris americana*. N. *Stigmaphyllon columbicum*. O. *Sapium glandulosum*. P. *Selenicereus megalanthus*. Q. *Sterculia apetala*. R. *Casearia* sp. 1. S. *Casearia* sp. 2. T. *Coccoloba uvifera*. U. *Maclura tinctoria*. V. *Tabebuia rosea*. W. *Randia aculeata*. X. *Pithecellobium dulce*.

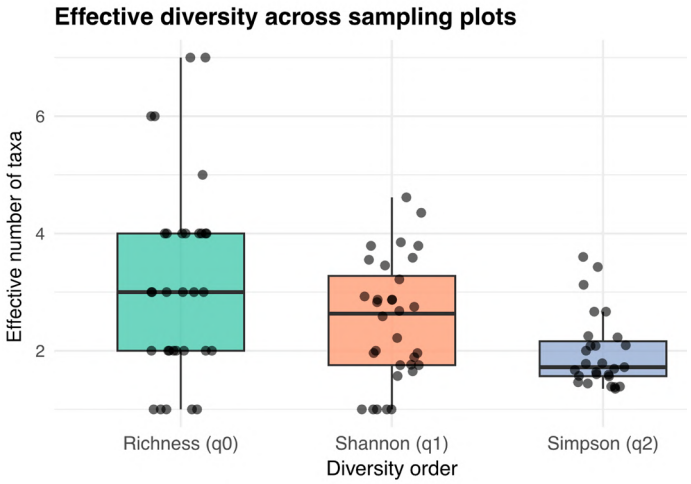

Figure 6. Distribution of effective plant diversity across 32 vegetation plots for Hill numbers q0 (taxon richness), q1 (exponential Shannon diversity), and q2 (inverse Simpson diversity). Points represent individual plots; boxes show the interquartile range, central lines indicate the median, and whiskers extend to 1.5 times the interquartile range.

the assemblage was equivalent to approximately 8 equally abundant taxa. Diversity of order 2 (q_2 = 5.74) reflected strong dominance.

The rank-abundance curve (Figure 4) showed a steep slope and a long tail of rare taxa. The dominant taxon was *Artibeus planirostris* (33.87%), followed by taxa with intermediate abundances such as *Sturnira tildae, Rhynchonycteris naso,* and *Phyllostomus discolor* (12.37% each), and taxa with intermediate to low abundances such as *Sturnira giannae* (6.99%), *Saccopteryx canescens* and *Glossophaga soricina* (5.38% each), and *Sturnira* sp. (4.30%). The remaining taxa had abundances between 1.61% and 0.54% and were considered rare.

During sampling, six recapture events were recorded for *A. planirostris* and *S. tildae*. Recaptures occurred among cells 1, 3, 5, and 6, indicating movements by individuals among different landscape covers. *Artibeus planirostris* was recaptured among cells 1, 3, and 5, whereas *S. tildae* was recaptured both within the same cell and among cells 1, 5, and 6.

Sampling coverage for the plant assemblage was relatively high (93.8%); however, the extrapolation curve continued to increase, indicating that additional plant taxa could be detected with greater sampling effort (Supplementary data SD3). Overall, 35 plant taxa were recorded (q_0 = 35). Effective diversity decreased to q_1 = 14.04 and q_2 = 9.98, indicating that the assemblage was dominated by a smaller subset of common taxa.

Representative plant taxa recorded in the study area are shown in Figure 5. Effective plant diversity varied across the 32 sampling plots (Figure 6). Taxon richness (q_0), exponential Shannon diversity (q_1), and inverse Simpson diversity (q_2) all differed among plots. Values of q_2 were consistently lower than q_0 and q_1, indicating that most plots were dominated by a few abundant taxa and had low evenness.

The floristic similarity dendrogram showed a clustering pattern associated with vegetation cover type. Plots located in pastures (sampling cells 2, 5, and 7) showed greater similarity to one another and formed well-defined groups.

Table 2. Composition and abundance of plant taxa recorded in the tropical dry forest study area of Puerto Mosquito, Cesar, Colombia.

Plant taxon	Abundance	Relative frequency (%)	Number of plots
Pithecellobium dulce	56	17.34	4
Randia aculeata	52	16.10	1
Guazuma ulmifolia	41	12.69	4
Maclura tinctoria	26	8.05	4
Casearia sp. 1	26	8.05	4
Morisonia americana	23	7.12	2
Coccoloba uvifera	22	6.81	4
Selenicereus megalanthus	17	5.26	1
Solanum aturense	8	2.48	1
Chloroleucon mangense	7	2.17	4
Enterolobium cyclocarpum	7	2.17	4
Stigmaphyllon columbicum	6	1.86	1
Mangifera indica	5	1.55	2
Malvaviscus arboreus	5	1.55	1
Sapium glandulosum	2	0.62	2
Bunchosia hartwegiana	1	0.31	1
Monilicarpa sp.	1	0.31	1
Carludovica palmata	1	0.31	1
Casearia sp. 2	1	0.31	1
Cecropia sp.	1	0.31	1
Ceiba pentandra	1	0.31	1
Citrus aurantium	1	0.31	1
Citrus limon	1	0.31	1
Croton sp.	1	0.31	1
Ficus dendrocida	1	0.31	1
Leguminosae	1	0.31	1
Malpighia glabra	1	0.31	1
Manilkara zapota	1	0.31	1
Melicoccus bijugatus	1	0.31	1
Eugenia sp.	1	0.31	1
Psidium guajava	1	0.31	1
Sterculia apetala	1	0.31	1
Tabebuia rosea	1	0.31	1
Tetrorchidium sp.	1	0.31	1
Triplaris americana	1	0.31	1

Similarly, plots corresponding to forest areas (sampling cells 6 and 8) tended to cluster together, indicating affinity in species composition. Plots located in transition zones (sampling cells 1, 3, and 4) showed intermediate clustering patterns, reflecting mixed floristic composition (Supplementary data SD4). Across all recorded plant taxa, *Pithecellobium dulce* (17.34%), *Randia aculeata* (16.10%), and *Guazuma ulmifolia* (12.69%) were the most abundant (Figure 7; Table 2). Of these, *Randia aculeata* and *Guazuma ulmifolia* were classified from the literature as potential bat food resources, whereas *Pithecellobium dulce* was included among other recorded plant taxa. The remaining taxa each represented 8.05% or less of the recorded individuals.

Diet and bat-plant interaction network. Seed types recorded in bat fecal samples were photographed (Figure

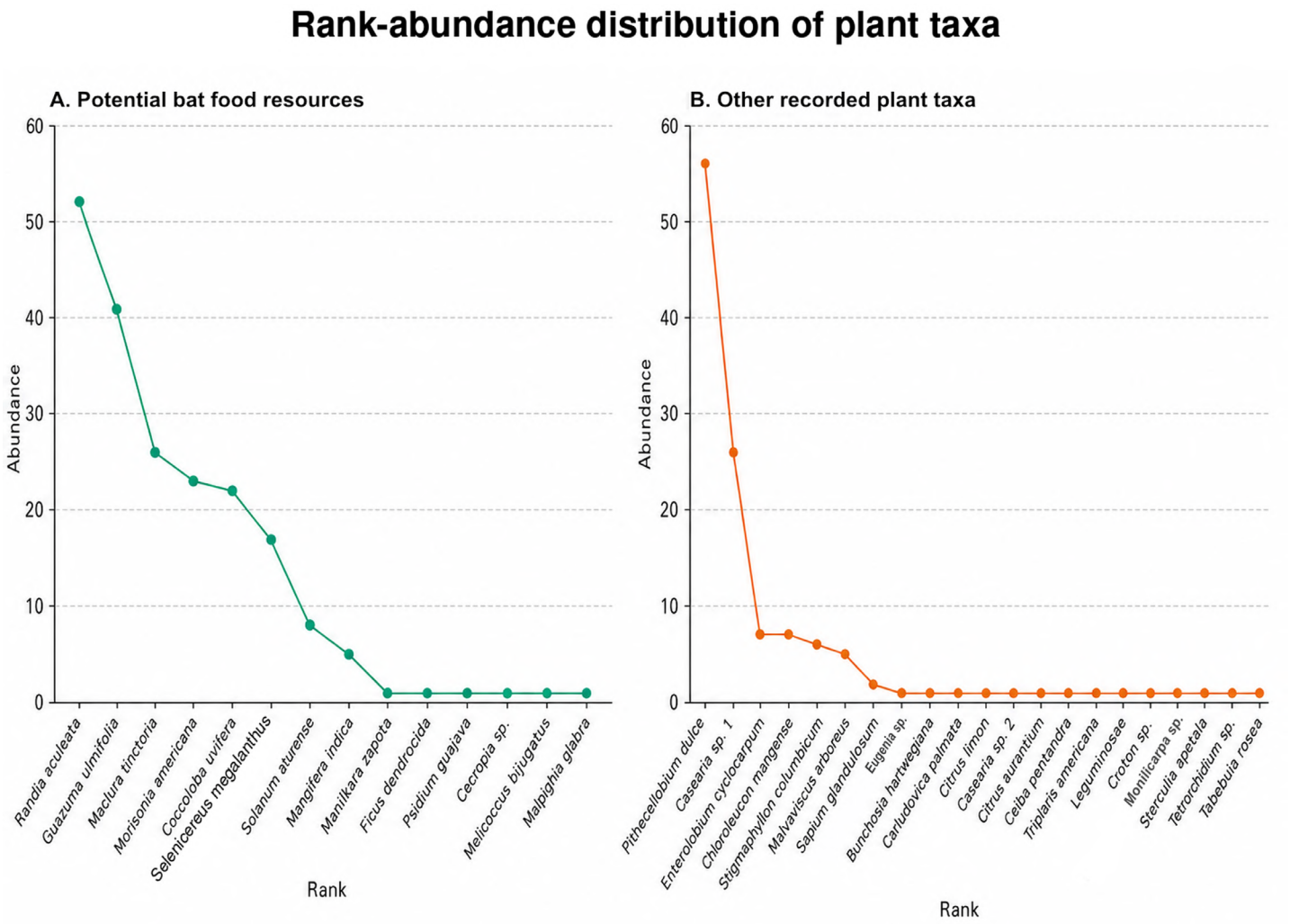

Figure 7. Rank-abundance curves of plant taxa recorded in the tropical dry forest of the study area: (A) potential bat food resources and (B) other recorded plant taxa, classified from published evidence of bat consumption. This classification is descriptive and does not imply that all taxa in panel A were consumed during this study.

8). The bat-plant interaction network included seven bat taxa with dietary evidence of fruit consumption and 11 plant taxa, with 26 unique bat-plant links recorded (Table 3). Two of these links, those involving *Mangifera indica* and *Manilkara zapota,* were supported by direct feeding observations; the remaining links were based on fecal evidence. Network connectance was 0.33, link density was 3.70, the mean number of links per taxon was 1.44, nestedness was 22.12, and network specialization was $H_2' = 0.38$ (Figure 9).

Interaction frequencies were highest for *A. planirostris* (25 records) and *S. tildae* (17 records), which were the bat taxa with the highest number of associations in the network. In contrast, *G. soricina* and *C. perspicillata* showed few interactions. Among the seed-based interactions summarized in Supplementary data SD5, *Piper* sp. was the most frequently recorded resource (17 records), followed by *Cissus* sp. (10 records) and *Muntingia calabura* (9 records). Supplementary data SD5 presents a reduced seed-based subset comprising six bat taxa and eight plant taxa and therefore shows five associations for *A. planirostris*. Degree values were calculated from the complete interaction network shown in Figure 9. In that complete network, *A. planirostris* had the highest degree of interaction (degree = 9), followed by *S. giannae* (degree = 5) and *S. tildae* (degree = 4). Among plants, *Piper* sp. had the highest number of associations (degree = 5), whereas *Cecropia* sp., *M. zapota, Solanum* sp. 2, and *Solanum* sp. 3 each showed a single interaction. The taxon-level specialization index (*d'*) was 0.56 for *Sturnira* sp., 0.45 for *S. tildae,* and 0.41 for *G. soricina,* compared with 0.12 for *P. discolor* and 0.15 for *C. perspicillata*. Among the six bat taxa included in the DII calculation, *A. planirostris* had the highest value (DII = 1.63), followed by *S. tildae* (DII = 0.52) and *S. giannae* (DII = 0.16). The other three

Table 3. Structural metrics of the bat-plant interaction network in the tropical dry forest of Puerto Mosquito, Cesar, Colombia.

Metric	Value
Number of bat taxa	7
Number of plant taxa	11
Number of observed links	26
Connectance	0.33
Nestedness	22.12
Link density	3.70
Links per taxon	1.44
Specialization (H_2')	0.38

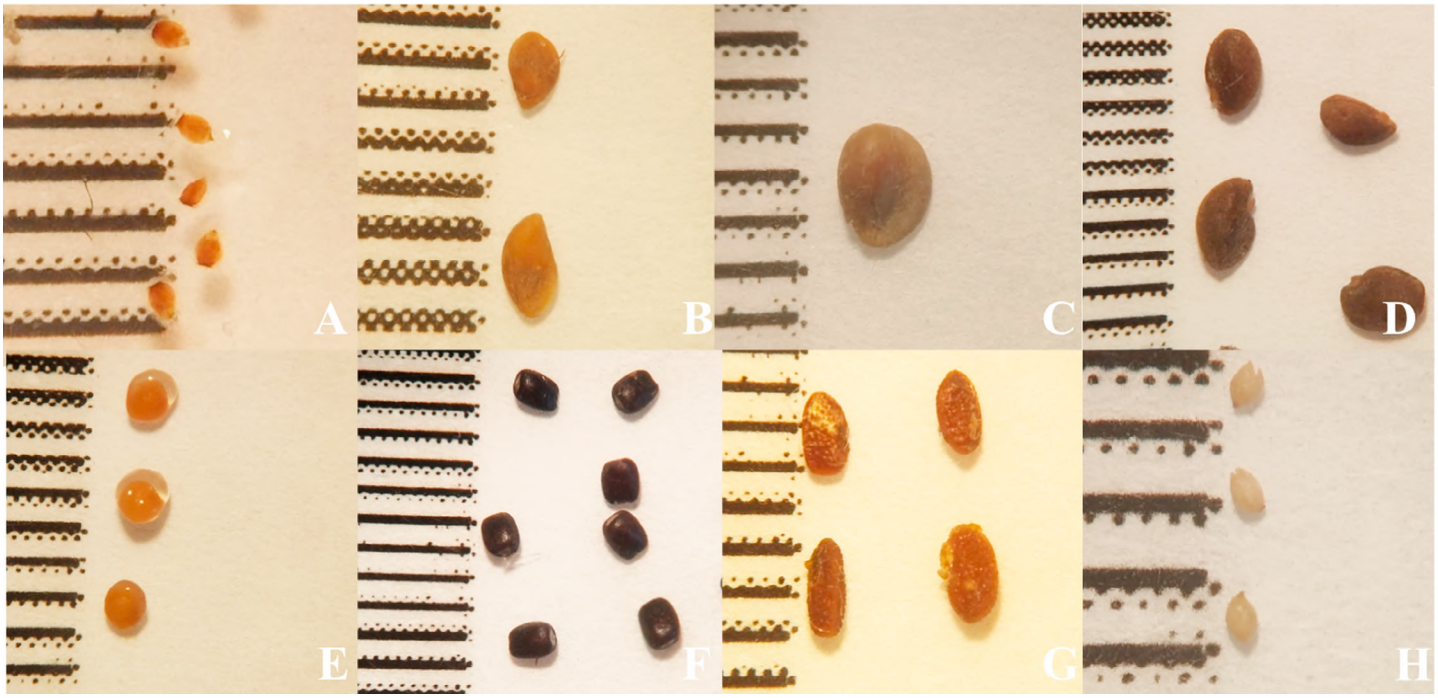

Figure 8. Photographic plate of seeds recovered from bat fecal samples. A. *Cissus* sp. B. *Solanum* sp. 3. C. *Solanum* sp. 2. D. *Solanum* sp. 1. E. *Ficus* sp. F. *Piper* sp. G. *Cecropia* sp. H. *Muntingia calabura*.

taxa had lower DII values (Supplementary data SD6).

Discussion

Bat assemblage structure. The composition of the bat assemblage recorded in this study is consistent with patterns reported for tropical dry forests, where species-rich assemblages are often associated with warm and seasonal environments (Vela Vargas and Pérez-Torres 2012; Pabón *et al.* 2023). The dominance of Phyllostomidae aligns with trends described for the Neotropics, where this family usually concentrates the greatest richness and relative abundance (Díaz *et al.* 2021). The marked dominance of *A. planirostris* agrees with previous studies in similar ecosystems (Calderón Acevedo 2012; Durán and Canchila Pérez 2015) and may be explained by its generalist habits and high capacity to adapt to disturbed environments (Ballesteros and Racero-Casarrubia 2012). This finding suggests that the bat assemblage structure is strongly influenced by species with greater ecological plasticity, which can exploit a broad range of available resources. The predominance of Phyllostomidae should also be interpreted considering the sampling methodology, as mist nets are particularly effective for capturing low-flying phyllostomid bats, whereas many aerial insectivorous species flying above the understory are underrepresented using this technique (Kunz and Parsons 2009).

The genus *Sturnira* showed the highest taxon richness, represented by *S. tildae, S. giannae,* and *Sturnira* sp.; *S. tildae* was among the most abundant taxa. This observation agrees with Ramos-Rodríguez *et al.* (2018). The high representation of this genus has been associated with environments showing some degree of disturbance, suggesting that its presence may be related to habitat perturbation and the availability of secondary resources (Medellín and Víquez 2014).

The low evenness observed in the bat assemblage suggests an unequal distribution of abundance, with a few species accounting for most individuals. This pattern has been widely reported for bat assemblages in fragmented tropical dry forest landscapes (Stoner 2005; Meyer *et al.* 2016). It may be associated with variation in resource availability and structural simplification of vegetation in disturbed habitats, factors that condition the availability of food, roosts, and perches (Galindo-González and Sosa 2003; Chazdon *et al.* 2007; Medina *et al.* 2007). Generalist species therefore tend to dominate because they can exploit a greater diversity of resources and move efficiently through heterogeneous matrices (Fleming 1988; Meyer *et al.* 2016), whereas species with more specific requirements may become restricted. The presence of many rare species may be related both to limitations in the availability of specific resources and to greater sensitivity to habitat transformation, because these species often depend on more stable environmental conditions or greater structural complexity of vegetation (Chazdon *et al.* 2007; Henry *et al.* 2007). Landscape configuration, including fragment isolation and the quality of the surrounding matrix, also influences how different species use space and access available resources (Meyer *et al.* 2016).

The recaptures recorded among sampling cells suggest that species such as *A. planirostris* and *S. tildae* actively use different vegetation covers within the fragmented landscape. This movement may favor ecological processes such as seed dispersal and functional connectivity in tropical dry forests. These patterns indicate that the structure of the bat assemblage responds not only to resource availability, but also to interactions among landscape heterogeneity,

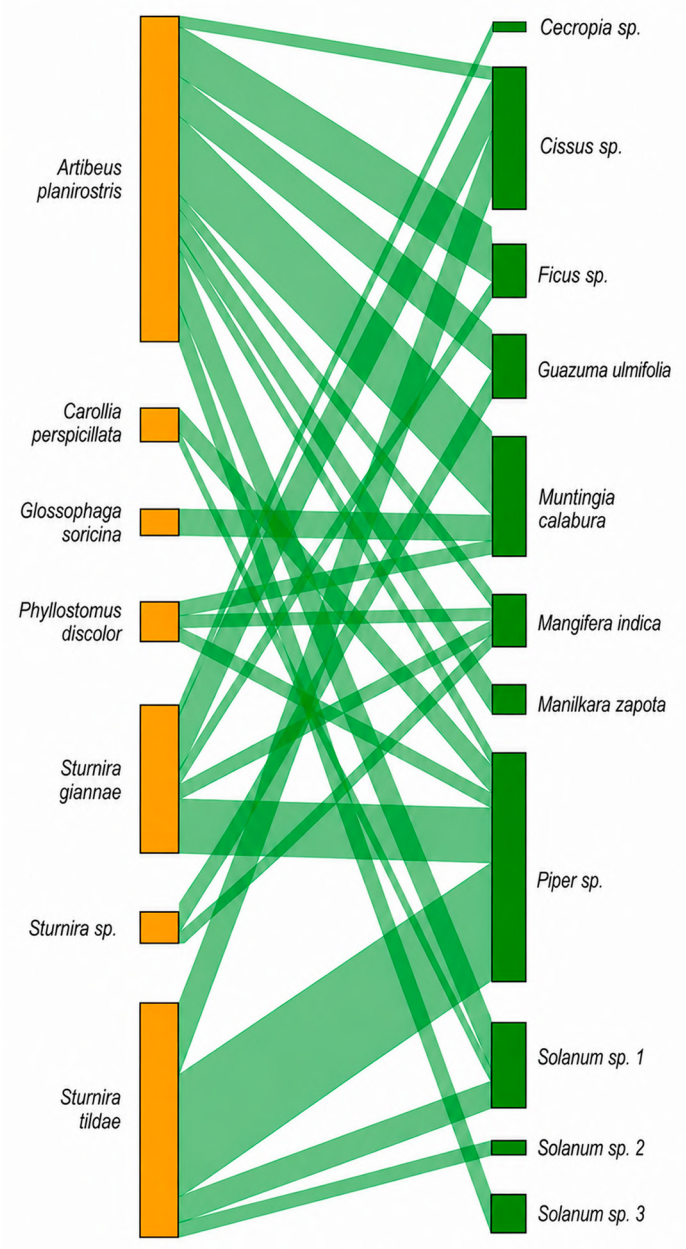

Figure 9. Quantitative bat-plant interaction network between seven bat taxa with documented fruit consumption and 11 plant taxa in the tropical dry forest of Puerto Mosquito, Cesar, Colombia. The network contains 26 unique bat-plant links: 24 were documented from dietary records in fecal samples, whereas the links involving *Mangifera indica* and *Manilkara zapota* were documented by direct field observations of fruit feeding. These two observations document fruit consumption but are not evidence of seed ingestion or dispersal. Link width represents interaction frequency. Bat abbreviations: A. p = *Artibeus planirostris*; C. p = *Carollia perspicillata*; G. s = *Glossophaga soricina*; P. d = *Phyllostomus discolor*; S. g = *Sturnira giannae*; S. sp. = *Sturnira* sp.; S. t = *Sturnira tildae*.

species-level ecological traits, and the levels of disturbance present in the study area. This highlights the role of bats as key functional components of fragmented ecosystems, where their dominance and composition may directly influence ecological processes such as seed dispersal and vegetation regeneration, even in productive matrices.

Frugivorous bats play a key functional role in tropical dry forests by dispersing seeds across heterogeneous and disturbed landscapes, thereby contributing to vegetation regeneration and ecological succession. These processes are particularly important in fragmented ecosystems, where seed dispersal can enhance connectivity among forest remnants and facilitate natural regeneration (Espejo and Morales 2019).

Plant assemblage and resource heterogeneity. The pattern observed in plant composition is consistent with reports for tropical dry forests, where families such as Fabaceae, Rubiaceae, and Malvaceae concentrate a large proportion of abundance. Other families such as Capparaceae, Polygonaceae, Cactaceae, and Moraceae were also recorded, coinciding with previous studies in this ecosystem (IAvH 1998; Carrillo-Fajardo *et al.* 2007; Acosta-Santos and Tatis-Salcedo 2019; Suárez-R and Vargas-R 2019). Similarly, the genera recorded in this study are comparable to those reported for tropical dry forests in the Caribbean region, particularly in the Magdalena River valley (Ruiz-V and Saab-R 2020). Plant assemblage structure showed strong dominance by few species, particularly *Pithecellobium dulce, Guazuma ulmifolia,* and *Randia aculeata,* a pattern similar to that documented by Ballesteros-Correa *et al.* (2019). The dominance of *P. dulce* may be associated with its frequent use in agricultural and livestock systems, where it provides shade for cattle and wood for fences (Monroy and Colín 2004; Hernández-Neri *et al.* 2021), favoring its establishment and high abundance in disturbed landscapes. This species also has high tolerance to drought, a trait that allows it to persist and dominate under tropical dry forest conditions (Rojas-Basto *et al.* 2015; Hernández-Neri *et al.* 2021).

Effective diversity values indicated low evenness in the plant assemblage, with a few taxa accounting for the largest proportion of individuals. This pattern, reflected in q_1 and q_2 values lower than q_0 across plots, indicates dominance by a subset of abundant taxa and is consistent with the uneven assemblage structure observed in the vegetation plots. The grouping of plots according to vegetation cover type reflects the heterogeneity of the study area, which results from fragmentation processes associated with anthropogenic activities. Differences in floristic composition among plots suggest taxon turnover at a local scale, indicating that diversity in this system depends not only on abundance, but also on spatial variation in composition. This variation may also be associated with the location of the sampling plots within the heterogeneous landscape, as the sampling cells included tropical dry forest remnants, transition zones, and pastures, each characterized by different levels of disturbance and vegetation structure. This pattern suggests that vegetation structure is influenced by land-use history and by variation in biotic and abiotic factors, as reported in other studies of fragmented tropical dry forest landscapes (Sardi *et al.* 2018; García-Q *et al.* 2021). Plant taxa classified from the literature as potential bat food resources were abundant but heterogeneously distributed among plots. Because fruit biomass was not measured, this pattern should be interpreted as spatial heterogeneity in locally recorded vegetation resources rather than as a quantitative estimate of food availability. The occurrence of families such as Moraceae, Solanaceae, and Cactaceae, which include

known bat food plants, nevertheless indicates the potential trophic relevance of the local plant assemblage.

Bat-plant interactions and functional implications. Ecological interactions between frugivorous bats and plants play a fundamental role in the dynamics and regeneration of tropical ecosystems, especially in fragmented environments where seed dispersal processes may be altered by landscape transformation (Muscarella and Fleming 2007). In this study, the interaction network showed a structure dominated mainly by bat taxa with high trophic plasticity, connectance of 0.33, and associations concentrated in few bats and plant resources. These patterns have been widely reported in tropical ecosystems, where resource availability, environmental heterogeneity, and anthropogenic disturbance directly influence the organization of mutualistic networks and the ecological functionality of disperser taxa (Aguilar-Garavito *et al.* 2014; Casallas-Pabón *et al.* 2017; Castaño *et al.* 2020). Within Stenodermatinae, several taxa usually consume plant resources characterized by fibrous fruits and poorly synchronized fruiting periods (Suárez Castro and Montenegro 2015). However, both in this study and in Sánchez *et al.* (2012), *A. planirostris* showed greater dietary plasticity than other species in the group. This species had the highest number of interactions in the network and was also highly abundant in the bat assemblage. Its generalist habits allow it to exploit a broad variety of plant resources, supporting a diverse diet that can adjust to *different environmental conditions*. The dominance of highly connected species in the network agrees with Velásquez Roa *et al.* (2023), who highlighted that generalist taxa may represent the functional core of mutualistic networks in fragmented ecosystems, maintaining seed dispersal flow even under disturbance. Similarly, Rodríguez-González *et al.* (2025) recorded assemblages dominated by generalist frugivorous bats and emphasized their importance in ecological succession and vegetation regeneration.

Studies conducted in Neotropical tropical dry forests have shown that these ecosystems support a diverse assemblage of frugivorous bats that contributes substantially to forest maintenance and regeneration through seed dispersal (Nassar *et al.* 2013). In particular, abundant canopy frugivores such as *A. planirostris* and *P. discolor* have been recognized as key dispersers because of their frequent interactions with chiropterochorous plants. In our study, *A. planirostris* was the dominant taxon and exhibited the highest disperser importance index, supporting its central ecological role within the bat–plant interaction network.

The network structure was shaped by the predominance of generalist taxa and the uneven distribution of interactions. *Artibeus planirostris* and *Sturnira tildae* concentrated many associations, whereas several plant and bat taxa had few links, a pattern that may contribute to the observed nestedness (22.12) and H_2' (0.38; Staniczenko *et al.* 2013). The genera *Ficus, Cecropia, Piper, and Solanum,* which Ramos-Rodríguez *et al.* (2018) associated with bats in disturbed habitats, were also represented in our network. *Piper* sp. was the most frequently recorded dietary resource, and its frequent use agrees with previous dietary studies and may be related to its temporal availability and energy content (Idárraga *et al.* 2016; Velásquez Roa *et al.* 2023). However, *Piper* sp., *Cissus* sp., and *Muntingia calabura* were not detected in the vegetation plots and may have originated from unsampled portions of the cells or nearby landscape elements, including riparian vegetation along the Magdalena River. Although their precise source cannot be determined, this mismatch is consistent with the mobility of fruit-feeding bats and their use of spatially heterogeneous resources (Ávila-Cabadilla *et al.* 2014). Consequently, our data document only partial correspondence between locally recorded plants and bat diet and do not constitute a direct test of resource selection or proportional use. The persistence of multiple interactions in this transformed landscape suggests that trophic plasticity and mobility may help maintain seed dispersal and ecological connectivity, although the magnitude of this contribution was not quantified directly (Castaño *et al.* 2020).

This study represents an initial assessment of interactions between fruit-feeding bats and plant resources in a heterogeneous tropical dry forest landscape. Some seeds could only be identified to genus or morphospecies because of taxonomic limitations and the availability of reference collections. Because vegetation sampling quantified standing plants rather than fruit biomass, the plant data should be interpreted as an index of locally recorded resources rather than a direct measure of fruit availability. In addition, the two bat-sampling campaigns represented one transitional period and one dry-season period, with unequal sampling effort (16 *vs.* 8 nights) and no temporal replication; campaign and climatic period were therefore confounded, and the data do not support seasonal inference. The occurrence of dietary resources such as *Piper* sp. outside the vegetation plots further indicates that bats used resources from portions of the landscape not represented by the plots. The interactions involving *Mangifera indica* and *Manilkara zapota* were based on direct observations of fruit feeding and therefore document trophic use of these fruits, but they should not be interpreted as direct evidence of seed dispersal. Future studies should incorporate replicated seasonal sampling, explicit phenological or fruit-biomass measurements, spatial analyses, and long-term monitoring to better understand resource selection, seed-dispersal dynamics, and the functional role of bats in tropical dry forest regeneration.

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Declaration of Artificial Intelligence use

During the preparation of this manuscript, artificial intelligence tools, specifically ChatGPT, were used only to support language editing, preliminary translation, and checking the concordance between in-text citations and the bibliography. The authors fully reviewed and edited the resulting text and assumed complete responsibility for the final content of the manuscript. No artificial intelligence tools were used to generate data, perform analyses, or formulate the study conclusions.

Author contributions

Mariana Velásquez-Trillos: designed the study, carried out the fieldwork, performed the data analyses and wrote and edited the manuscript. L. Roberto Sánchez Montaño: designed the study, supported the processing and identification of plant and seed material and reviewed the manuscript. Juan David González-Alvarez: participated in field activities, supported methodological development, and contributed to the identification of biological material. Aldemar A. Acevedo Rincón: designed the study, performed the data analyses and wrote and edited the manuscript, and directed and supervised the research and guided the interpretation of the results. All authors reviewed and approved the final version of the manuscript.

Supplementary data

SD1. Darwin Core records of bat voucher specimens collected during the study and deposited in the mammal collection of the Museo de Ciencias Naturales José Celestino Mutis, Universidad de Pamplona. Taxa that could not be confirmed to species are reported at the genus level.

SD2. Darwin Core records of botanical voucher specimens collected during the study and deposited in the Herbario Catatumbo Sarare (HECASA).

SD3. Sample-size-based rarefaction (solid line) and extrapolation (dashed line) of plant taxon richness (q_0) as a function of the number of individuals. The filled circle marks the observed reference sample, and the shaded area represents the 95% confidence interval.

SD4. Hierarchical clustering dendrogram of floristic dissimilarity among the 32 vegetation plots based on Jaccard distance. Lower Jaccard distances indicate greater similarity in taxonomic composition.

SD5. Heatmap of the reduced seed-based interaction subset recovered from bat fecal samples for six bat taxa and eight plant taxa. Darker shading indicates higher interaction frequency. This subset was not used to calculate degree values for the complete network shown in Figure 9. Bat abbreviations follow Figure 9.

SD6. Disperser Importance Index (DII) for the six bat taxa included in this analysis, calculated from bat relative abundance and the percentage of fecal samples containing seeds. Direct feeding observations involving *Mangifera indica* and *Manilkara zapota* were excluded from the DII calculation.

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