

Taxonomic and functional responses of bat communities along an urbanization gradient in a Neotropical transition zone

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Abstract

Rapid urban expansion in the Neotropics has transformed natural landscapes, imposing environmental filters that drastically alter local biodiversity. This study evaluated the taxonomic and functional responses of bat communities along an urbanization gradient in the city of Culiacán, Sinaloa, Mexico. Between January and September 2024, four sites with contrasting landscape configurations were monitored via mist nets. In total, 537 individuals representing 26 species were recorded. Our results revealed strong environmental filtering: while species richness decreased markedly in the urban core (${}^0D = 6.5$) compared with the control site (${}^0D = 23.5$), total abundance increased significantly within the city, driven by the hyperdominance of the generalist frugivore *Artibeus jamaicensis* (83.2% of urban captures). Functionally, urbanization led to the loss of aerial and narrow-space insectivorous guilds, thereby strongly favoring species with high mobility and trophic plasticity. The ordination analyses identified urban land cover as the primary driver of community structure ($R^2 = 0.99$). A key finding was the contrasting ecological roles of peri-urban edges: remnants of native vegetation (Cerritos) served as refuges, preserving taxonomic identity by retaining sensitive specialists such as *Natalus mexicanus*, whereas areas dominated by managed vegetation supported tolerant species but failed to conserve the original diversity. Overall, Culiacán is undergoing an advanced process of biotic homogenization. Conservation of local bat fauna requires planning strategies that go beyond simple tree-planting initiatives, prioritizing the strict protection of peri-urban native vegetation patches and the design and implementation of structurally complex ecological corridors to restore landscape functional connectivity.

Introduction

Urbanization represents one of the most profound processes of landscape transformation globally (Grimm et al., 2008; Buettner, 2015). The replacement of vegetation cover by impervious surfaces drives the fragmentation of natural habitats and alters matter and energy flow, creating ecosystems with unique dynamics (Pickett et al., 2001; Alberti, 2005). Currently, 55% of the global population resides in urban areas, a figure projected to increase to 68% by 2050 (United Nations, 2019). This growth poses a critical challenge to biodiversity, as it signifies a significant decline in native species richness and an accelerated loss of natural habitats in the coming decades (Seto et al., 2012; Li et al., 2022).

According to Keddy (1992), the environmental filtering hypothesis states that local community structure results from the selective elimination of species from a regional pool that lack the physiological or morphological traits necessary to tolerate the abiotic conditions of the sites. Under this conceptual framework, cities function as strong environmental filters that select species based on their functional attributes (Crocì et al., 2008; Swan et al., 2021). Thus, biological communities respond to multiscale factors such as city size and, crucially, the quality and composition of green infrastructure (Téllez-Hernández et al., 2023). However, habitat fragmentation due to urbanization often triggers phenomena such as species movement toward areas where their vital requirements persist. Consequently, while many sensitive species are driven to conserved habitats (McKinney, 2002), others find ecological opportunities in cities that allow them to effectively coexist with humans (Abramova, 2010; Korine et al.,

2022). This differential process leads to biotic homogenization, wherein urban communities lose their specialist species and become globally dominated by a few “winner” generalist species (McKinney, 2006).

One of the taxa most sensitive to these changes is the order Chiroptera. Although their richness and diversity vary depending on the degree of urbanization (Gutiérrez-Granados & Rodríguez-Zúñiga, 2024), response patterns depend on trait-based environmental filtering (Jung & Threlfall, 2018). Global studies indicate a greater urban affinity in species with wing morphology adapted to open spaces, low-frequency echolocation, and plasticity in roost use (Wolf et al., 2022). In contrast, closed-habitat species are displaced by barriers such as anthropogenic noise and light pollution (Russo & Ancillotto, 2015; Moretto & Francis, 2017). This differential sensitivity suggests bats as high-potential bioindicators of urban habitat quality (Li & Kalcounis-Rueppell, 2018; Gili et al., 2020).

In Mexico, bats' response to disturbances caused by urban transformation presents striking contrasts. While cities in the southern part of the country act as refuges sustaining high taxonomic richness (Briones-Salas et al., 2024), in the west, the assemblage biomass is dominated by large frugivores of the genus *Artibeus* (Ramírez-Silva & Lugo-Gil, 2020). In contrast, in the arid north, urban ecology revolves around colonies of aerial insectivores such as *Tadarida brasiliensis* (Rivera-Villanueva & Dalaí-López, 2023). This heterogeneity of responses underscores the need to generate context-specific data for each urban area, as cities function as novel ecosystems where the historical and geographical configuration of the landscape uniquely modulates biodiversity (Niemelä, 1999; McDonnell & Hahs, 2008). This is particularly critical for understanding dynamics in biogeographical transition zones where the Nearctic and Neotropical regions converge, as is the case in the state of Sinaloa (Morrone, 2019).

In this region, the city of Culiacán constitutes a strategic node for ecological research, not only because of its demographic relevance as the most populated city in the state, with 808,416 inhabitants (INEGI, 2021a), but also because of its critical location at the northwestern edge of the Neotropical region (Alves et al., 2018). The urban development of a city is spatially constrained by extensive areas of intensive agriculture and remnants of tropical dry forest, encompassing both secondary succession stages and mature vegetation (Borbolla-Gaxiola et al., 2024) and configuring a highly heterogeneous landscape matrix. Under this scenario, these land covers are expected to act as differential ecological filters along the urbanization gradient; therefore, analyzing how landscape composition influences bat diversity is key to understanding the magnitude of anthropogenic impacts in developing Neotropical cities (Santos Bezerra & Bocchiglieri, 2024).

The objective of this study was to evaluate the taxonomic and functional composition of the bat community along an urbanization gradient and to determine how landscape structure explains the dissimilarity among sites. Based on environmental filtering theory and the regional context, it is hypothesized that 1) species richness and functional diversity will drastically decrease at sites with higher urban cover than at the control site; 2) the urban community will be dominated by highly mobile generalist frugivores (such as those of the genus *Artibeus*), resulting in biotic homogenization; and 3) the

presence of remnant native vegetation patches will buffer these effects, allowing the presence of sensitive and habitat-dependent species.

Materials and methods

Study area. The study was conducted in the municipality of Culiacán, including its peri-urban zone, which is in the biogeographical transition zone of northwestern Mexico. The region features an extremely hot semiarid climate [BS₁ (h') w (w) (e)] according to the Köppen climate classification modified by García (2004), with a summer monsoon rainfall regime and a mean annual temperature of 26°C (UAS, 2020). The original landscape matrix, dominated by tropical dry forest, has been historically fragmented by intensive agriculture and urban expansion (Borbolla-Gaxiola et al., 2024).

Sampling design and site selection. An urbanization gradient comprising four sites with contrasting landscape configurations was established to evaluate the effect of urban environmental filtering on the bat community (Fig. 1).

- **Control (Guayabos; 25.1750° N, -107.2055° W):** A reference site located in the Sierra Madre Occidental, > 40 km from the city, representative of conserved native vegetation (tropical dry forest and riparian gallery forests) with minimal apparent anthropogenic disturbance.
- **Peri-urban forest transition (Cerritos; 24.8625° N, -107.4278° W):** Located on the northern edge, although it borders the urban footprint, it maintains structural connectivity with continuous remnants of tropical dry forest.
- **Urban (Jardín Botánico; 24.8237° N, -107.3854° W):** A site immersed in the central urban matrix, characterized by a high density of gray infrastructure, light pollution, and vegetation dominated by exotic and ornamental species.
- **Peri-urban agricultural transition (Primavera; 24.7160° N, -107.4011° W):** Located on the southwestern edge of the city, it presents a heterogeneous mosaic of residential development, water bodies, and patches of regenerating vegetation.

Landscape characterization. Landscape composition was quantified within a 3 km radius buffer area (28.6 km²) around each sampling point, a scale selected to encompass the average foraging range of Neotropical bats (Morrison, 1978; Saldaña-Vázquez et al., 2010). We used High-resolution PlanetScope satellite imagery (3-m spatial resolution; Planet Labs, 2024), specifically the surface reflectance product (level 3B), to ensure radiometric consistency. Image selection followed strict atmospheric quality criteria (< 10% cloud cover) and a phenological differentiation strategy: images from the dry season (March–May) were prioritized. During this period, native vegetation exhibited leaf senescence, whereas managed vegetation maintained high photosynthetic activity due to irrigation, which allows for optimal spectral contrast in the NDVI. Using supervised classifications, four land cover classes were distinguished: urban areas, which group all impervious surfaces (buildings, roads, industrial zones, and paved ground); 2) managed vegetation, defined as green areas dependent on anthropogenic irrigation (public parks and gardens as well as agricultural valleys); 3) native vegetation, corresponding to remnants of tropical dry

forest and gallery vegetation associated with rivers; and 4) water, including natural and/or artificial surface water bodies. Finally, the classification accuracy was validated through cross-analysis with official vector cartography (INEGI, 2021b) and corroborated through field verification to ensure a correct class assignment.

Bat sampling. We conducted a one-night-a-month monitoring protocol from January to September 2024. At each sampling site, five mist nets (12 × 2.5 m) were set at the understory level and operated for five hours beginning at dusk. Full moon periods and adverse weather conditions were avoided to minimize biases associated with lunar phobia and detectability (Pech-Canché et al., 2018). We also follows the criteria of Straube and Bianconi (2002) to standardize the sampling effort, and was calculated as the product of the total net area (m²), hours of exposure, and number of nights.

Captured individuals were identified *in situ* to the species level via specialized keys (Medellín et al., 2008; Ceballos, 2014; Álvarez-Castañeda et al., 2017). Following the ethical guidelines of the American Society of Mammalogists (Sikes et al., 2016) and under the scientific collection permit SPARN/DGVS/10573/23, all the samples were processed and released at the capture site.

Functional characterization. To evaluate changes in the functional structure of the bat community, a functional trait matrix was constructed for all recorded species (see Supplementary Table 1). Trait values were obtained through a review of specialized literature on Mexican mammals and global databases, encompassing three complementary ecological dimensions:

1. **Trophic dimensions:** Trophic guilds were assigned based on primary diet (e.g., frugivore, insectivore, nectarivore) and trophic level, following the hierarchical classification of González-Salazar et al. (2014) and corroborated with the EltonTraits 1.0 database (Wilman et al., 2014).
2. **Foraging strategies and echolocation:** Species were categorized according to their habitat use and relationship with clutter (physical obstacles) following Denzinger and Schnitzler (2013). The categories included open-space, edge-space, and narrow-space foragers. Additionally, for insectivorous species, the peak frequency (kHz) of echolocation calls, obtained from the acoustic compendium by Ortega et al. (2022), was included as a key quantitative trait for prey detection. For species in the family Phyllostomidae, this variable was not assigned, as they use mixed sensory strategies (olfaction/vision).
3. **Morphological traits and life history:** Average quantitative variables for Mexican populations were incorporated: body mass (g) and forearm length (mm), extracted from Ceballos et al. (2014). Furthermore, categorical variables determining their persistence in anthropized environments were included: primary roost type (e.g., cave-dwelling, tree-dwelling, anthropogenic) and mobility capacity (sedentary, migratory, intermediate mobility), classified according to Ceballos et al. (2014) and Wilman et al. (2014).

Data analysis. Inventory completeness was evaluated via rarefaction and extrapolation curves based on sample coverage (Chao & Jost, 2012), implemented in the *iNEXT* package (Hsieh et al., 2016). Sampling

was considered satisfactory upon reaching 90% coverage, in accordance with the criterion of Moreno and Halffter (2000).

The community structure was analyzed as follows:

1. **Alpha diversity:** Hill numbers (${}^qD$) were calculated to quantify species richness ($q = 0$), common species ($q = 1$), and dominant species ($q = 2$).
2. **Abundance hierarchy:** Rank-abundance curves (Whittaker plots, 1965) were constructed via $\log_{10}$ -transformed abundances to visualize dominance patterns.
3. **Multidimensional functional diversity:** To quantify the breadth and structure of the functional niche of the assemblages, three complementary indices were calculated: functional richness (FRic), which measures the volume of the functional space occupied by the community; functional evenness (FEve), which describes the regularity in the distribution of abundances within this space (Villéger et al., 2008); and functional dispersion (FDis), which estimates the mean distance of species to the centroid of the community, weighted by their abundance (Laliberté & Legendre, 2010). These analyses were performed via the Gower distance to handle mixed traits (qualitative and quantitative) via the dbFD function in R (Laliberté et al., 2014).
4. **Dissimilarity and relationship with the landscape (beta diversity):** To evaluate the turnover in the composition and structure of the assemblages among sites, a principal coordinate analysis (PCoA) was performed. This analysis was based on a dissimilarity matrix calculated via the quantitative Ruzicka index, following the recommendations for abundance data by Legendre and Legendre (2012). To determine the influence of landscape composition on community structure, land cover variables (urban area, native vegetation, managed vegetation, and water bodies) were projected as environmental vectors onto the PCoA ordination space. The fitting of these vectors was performed via the envfit function from the *vegan* package (Oksanen et al., 2024), which evaluates the statistical significance ($p < 0.05$) of the correlation between each landscape variable and species composition via a Monte Carlo permutation procedure (999 permutations).

All statistical analyses and graphics were performed in the R environment (R Core Team, 2025).

Results

Landscape composition analysis revealed a marked gradient of urbanization and vegetation cover across the sampled sites. The Jardín Botánico site was characterized by the highest percentage of urban area (62.6%) and managed vegetation (32.3%), relegating native vegetation and water bodies to a marginal proportion (2.7% and 2.4%, respectively). In Primavera, although the matrix remained dominated by managed vegetation (47.7%), a transition toward more natural land cover was observed, with an increase in native vegetation (26%) and a reduction in urban patches (20.3%). Additionally, this site presented the highest water body cover (6%) across the entire gradient. Cerritos exhibited the most heterogeneous cover, highlighting a greater proportion of native vegetation (48.4%) coexisting beside managed vegetation (35.5%) and a smaller urban area (15.7%), and a minimal proportion of water bodies (0.4%).

Finally, the control site (Guayabos) included a landscape with a high degree of conservation, where native vegetation patches predominated (94.3%), anthropogenic elements, such as managed vegetation (5.3%), as well as urban areas and water bodies (0.2% each), were practically nonexistent.

The cumulative sampling effort was 6,750 h·m² per site, producing 27,000 h·m² for the study area. In total, 537 bats were captured, representing 26 species from 18 genera and five families. Phyllostomidae dominated the assemblage, accounting for 91.4% of captures (n = 491), followed by Mormoopidae (3.4%) and Molossidae (2.2%). The assemblage was strongly dominated by the generalist frugivore *A. jamaicensis*, accounting for 64.1% of total captures (n = 344). The next most abundant species were *A. lituratus* (6.3%, n = 34), *G. mutica* (5%, n = 27), and *A. hirsutus* (4.8%, n = 26). The remaining taxa occurred at very low frequencies: indeed, over half of the recorded species (53.8%, 14 of 26 taxa) were rare or incidental, represented by fewer than 5 individuals each (i.e., *L. xanthinus*, *C. senex*, and *M. rufus*; Table 1).

Table 1

Taxonomic composition and absolute abundance of bat species recorded at the four study sites.

Taxon (Family/Species)	JB	CE	PR	GU	Total
Phyllostomidae					
<i>Artibeus hirsutus</i> (K. Andersen, 1906)	0	0	11	15	26
<i>Artibeus jamaicensis</i> (Leach, 1821)	249	28	50	17	344
<i>Artibeus lituratus</i> (Olfers, 1818)	27	1	5	1	34
<i>Artibeus toltecus</i> (Saussure, 1860)	0	0	0	7	7
<i>Centurio senex</i> (Gray, 1842)	0	0	0	1	1
<i>Chiroderma scopaeum</i> (Handley, 1966)	0	0	0	4	4
<i>Dermanura phaeotis</i> (Miller, 1902)	0	0	0	10	10
<i>Sturnira parvidens</i> (Goldman, 1917)	0	3	10	7	20
<i>Choeronycteris mexicana</i> (Tschudi, 1844)	0	0	0	2	2
<i>Glossophaga mutica</i> (Merriam, 1898)	17	3	0	7	27
<i>Leptonycteris yerbabuenae</i> (Martínez y Villa, 1940)	3	0	0	2	5
<i>Desmodus rotundus</i> (E. Geoffroy, 1810)	0	0	0	11	11
Molossidae					
<i>Molossus rufus</i> (E. Geoffroy, 1805)	0	0	0	1	1
<i>Nyctinomops macrotis</i> (Gray, 1840)	0	0	0	3	3
<i>Tadarida brasiliensis</i> (L. Geoffroy, 1824)	0	0	0	8	8
Vespertilionidae					
<i>Lasiurus frantzii</i> (Peters, 1870)	0	0	0	1	1
<i>Lasiurus xanthinus</i> (Thomas, 1897)	1	0	0	0	1
<i>Myotis californicus</i> (Audubon y Bachman, 1842)	0	0	0	1	1
<i>Myotis fortidens</i> (Miller y Allen, 1928)	0	0	0	2	2
<i>Myotis velifer</i> (J.A.Allen, 1890)	0	1	0	0	1
<i>Rhogeessa parvula</i> (H. Allen, 1866)	2	3	0	2	7
<i>Parastrellus hesperus</i> (H.Allen, 1864)	0	0	0	2	2
Abbreviations: JB = Jardín Botánico; CE = Cerritos; PR = Primavera; GU = Guayabos. The taxonomic arrangement follows Medellín et al. (2008), Ceballos (2014), and Álvarez-Castañeda et al. (2017).					

Taxon (Family/Species)	JB	CE	PR	GU	Total
Mormoopidae					
<i>Pteronotus davyi</i> (Gray, 1838)	0	0	1	0	1
<i>Pteronotus mexicanus</i> (Miller, 1902)	0	2	0	13	15
<i>Pteronotus personatus</i> (Wagner, 1843)	0	0	2	0	2
Natalidae					
<i>Natalus mexicanus</i> (Miller, 1902)	0	1	0	0	1
Total	299	42	79	117	537
Abbreviations: JB = Jardín Botánico; CE = Cerritos; PR = Primavera; GU = Guayabos. The taxonomic arrangement follows Medellín et al. (2008), Ceballos (2014), and Álvarez-Castañeda et al. (2017).					

Bat abundance exhibited striking spatial heterogeneity across the sampling sites. The Jardín Botánico site had the highest absolute abundance, accounting for 55.7% of all captures ($n = 299$). This pattern was driven by the pronounced local dominance of *A. jamaicensis* (representing 83.2% of individuals at this site). Guayabos recorded the second-highest abundance ($n = 117$; 21.8%), notable for harboring exclusive families (Molossidae and Vespertilionidae) that were virtually absent from the urban environment. Finally, the Primavera and Cerritos sites exhibited the lowest abundances ($n = 79$ and $n = 42$, respectively), sustaining fewer individuals of common species, such as *A. jamaicensis* and *S. parvidens*, than the other sites did.

Functional analysis revealed the numerical dominance of the frugivorous guild, which accounted for 83.1% of the sample ($n = 446$). The remaining trophic groups occurred in markedly lower proportions: insectivores (8.6%, $n = 46$), nectarivores (6.3%, $n = 34$), and sanguivore (2%, $n = 11$). With respect to habitat use, this composition translated into an overwhelming prevalence of narrow-space foragers (95%, $n = 510$). Conversely, open-space and edge-space bats constituted a marginal fraction (5%, $n = 27$) and exhibited a highly restricted spatial distribution. Specifically, Guayabos site held 85.2% of all aerial and edge space insectivore bat records ($n = 23$), whereas these groups accounted for 1% of the local abundance at Jardín Botánico ($n = 3$).

The evaluation of bat sampling effort via coverage-based rarefaction curves indicated high inventory completeness across the four study sites (Fig. 2). The accumulation curves reached an asymptote at all locations, yielding sample coverage values above 0.90 (i.e., > 90% completeness). This finding indicates that the probability of detecting unseen species with additional sampling effort is minimal. Despite differences in community structure, both the most species-rich site (Guayabos) and the most heavily dominated site (Jardín Botánico) presented comparable levels of sampling saturation, thereby validating the robustness of the subsequent diversity comparisons.

True diversity analysis (Hill numbers, ${}^qD$) revealed a systematic simplification of the bat community structure across the urbanization gradient (Fig. 3). Compared with the urbanized sites, the conserved site Guayabos maintained significantly greater diversity across all orders ($q = 0, 1, 2$), as indicated by the nonoverlapping 95% confidence intervals. In terms of estimated species richness ($q = 0$), Guayabos presented an asymptotic estimate of 23.5 effective species; this value decreased by 47% in Cerritos (12.4) and plummeted by 72% in both Primavera and Jardín Botánico (6.5 effective species each). This negative trend intensified for common species diversity ($q = 1$). The high evenness in Guayabos (16.1) contrasted sharply with the drastic reductions observed elsewhere: Cerritos (4.0) and Primavera (3.3) presented low values, whereas Jardín Botánico reached a minimum of 1.9 effective species. Finally, dominant species diversity ($q = 2$) corroborated the extreme inequality within the city core. Guayabos maintained high structural diversity (13.0), the Jardín Botánico assemblage collapsed to 1.4 effective species, directly reflecting the absolute dominance of *A. jamaicensis*.

Functional structure analysis revealed distinct response patterns to urbanization. FDis exhibited the clearest linear simplification along the gradient: Guayabos presented the highest trait heterogeneity (0.3389), which steadily declined through Cerritos (0.2978) and Primavera (0.2014), reaching a minimum of 0.1172 at Jardín Botánico. Concurrently, compared with Guayabos (0.0027), FRic underwent a drastic contraction in occupied functional volume. This functional space decreased by an order of magnitude in Cerritos (0.00018) and Jardín Botánico (0.00014), with Primavera experiencing the most extreme compression (2.82×10^{-7}). Finally, functional evenness (FEve) displayed a nonlinear trend; the abundance distribution within the functional space was most regular at the peri-urban sites, Cerritos (0.7109) and Primavera (0.6943), surpassing the control site, Guayabos (0.6650). Conversely, Jardín Botánico recorded the lowest evenness for this attribute (0.3286).

Rank-abundance curves revealed stark structural contrasts among the assemblages (Fig. 4). Guayabos presented the longest curve with the shallowest slope, reflecting greater evenness in abundance distribution and a substantial contribution of rare species within the distributional tail. In contrast, the Jardín Botánico and Primavera curves displayed steep slopes with a precipitous initial drop. This pattern visually corroborates the low evenness at these sites, driven by the overwhelming dominance of the rank-1 species (*A. jamaicensis*). Finally, Cerritos produced a shorter curve indicative of lower species richness and simplified structure relative to Guayabos; even so, it maintains a better-balanced abundance distribution than either Jardín Botánico or Primavera.

Ordination analysis (PCoA) based on Ruzicka dissimilarity accounted for 79.7% of the total variation in its first two axes. The first axis (PCoA 1) explained 45.81% of the variance, graphically separates the sites along the land-use gradient, whereas the second axis (PCoA 2) explained 33.9% of the variance (Fig. 5). The dissimilarity matrix revealed that the highest degree of community turnover occurred between the most contrasting extremes of the gradient: Jardín Botánico and Guayabos (0.925). This was followed by comparisons between the urban core and the intermediate sites, which yielded elevated dissimilarity values against Cerritos (0.889) and Primavera (0.830). A lower range of differentiation was observed when the transitional sites were paired with the control site (Cerritos vs. Guayabos: 0.786; Primavera vs.

Guayabos: 0.775). Ultimately, the lowest dissimilarity was recorded between the two transitional sites, Cerritos and Primavera (0.640). Driving these structural shifts, the vector-fitting analysis (envfit) demonstrated that the urban area presented the highest and only statistically significant coefficient of determination ($R^2 = 0.99$, $p = 0.04$). The vector for this variable was positively oriented toward the Jardín Botánico site. A high coefficient ($R^2 = 0.96$) was observed within Native vegetation, indicating the exact opposite direction of urbanization, but this result was not significant ($p = 0.16$). Finally, Managed Vegetation ($R^2 = 0.89$, $p = 0.33$) and Water Bodies ($R^2 = 0.34$, $p = 0.75$) were not significantly correlated with site ordination.

Discussion

The assessment of sampling completeness confirms the robustness of the observed patterns. The sample coverage curves indicated high completeness across all the sites ($C_{min} = 0.93$ at Cerritos; $C_{max} = 0.99$ at Jardín Botánico). This suggests that the drastic reduction in richness recorded within the urban matrix is not an artifact of undersampling, but rather a true biological phenomenon reflecting severe community simplification. Our findings demonstrate an inverse relationship typical of urbanization gradients: a substantial decline in species richness at Jardín Botánico ($S = 6$) compared with Guayabos ($S = 21$) was juxtaposed with an increase in total abundance ($n = 299$ vs. $n = 117$). When using Hill numbers to analyze community structure, we quantified the magnitude of this functional collapse: the control site (Guayabos) supported a significantly greater diversity of common (${}^1D = 16.1$) and dominant (${}^2D = 13.0$) species than did the urban sites. In contrast, Jardín Botánico presented minimal values (${}^1D = 1.9$; ${}^2D = 1.4$), indicating that urbanization in Culiacán has reduced effective diversity by nearly an order of magnitude. This pattern is consistent with the biotic homogenization hypothesis, wherein specialist species are filtered out by urbanization, thereby favoring the proliferation of a few generalist “winner” species (McKinney, 2006; Pérez-Jiménez et al., 2025).

The urban bat community in Culiacán exhibited marked inequality in terms of abundance distribution, as evidenced by the steep slopes of the rank–abundance curves. The numerical dominance of *A. jamaicensis* (83.2%) and *A. lituratus* (9%) at Jardín Botánico reinforces the trends observed in other Neotropical cities, where these frugivores dominate urban biomass due to their ecological plasticity in such systems (Nunes et al., 2017; Ramírez-Silva & Lugo-Gil, 2020). The success of *Artibeus* species within the urban matrix is driven not only by their flight capacity and trophic flexibility to exploit ornamental patches, but also by adjustments in reproductive phenology. Recent research suggests that urban frugivorous bats can advance parturition and prolong reproductive periods by capitalizing on the urban heat island effect and constant food availability (Weinberg et al., 2025). This plasticity adjusts reproductive timing in response to climatic variability and is widely recognized (Ocampo-González et al., 2023); specifically, increases in ambient temperature have been associated with accelerated reproductive responses, which are often underestimated in global change scenarios (Festa et al., 2023).

The high abundance recorded specifically at Jardín Botánico suggests that this site functions as a stable resource patch. This aligns with Saldaña-Vázquez et al. (2010) findings on agroforestry landscapes,

which showed that, unlike small-bodied bats (*Sturnira*), the abundance of *Artibeus* species remains unaffected by habitat modification because of their high mobility and canopy foraging capabilities. Similarly, in Culiacán, this capacity enables *A. jamaicensis* and *A. lituratus* to effectively exploit the resources of Jardín Botánico, circumventing the seasonal energetic constraints of the surrounding tropical dry forest. However, this high population density poses latent risks; seemingly favorable urban environments can become “ecological traps” if the nutritional quality of resources is poor or if high density facilitates the transmission of parasites and diseases, thereby compromising the long-term viability of these populations (Vlaschenko et al., 2019; Bezerra & Bocchiglieri, 2023).

In stark contrast to the high-density urban scenario, the control site (Guayabos) stands out as a reservoir of ecological integrity and biodiversity. The persistence of the structural complexity typical of the tropical dry forest at this site promotes greater richness, evenness, and functional diversity, allowing for the coexistence of specialized guilds that are otherwise filtered out by the urban environment. The loss of these habitats would compromise essential ecosystem services, particularly agricultural pest control, as well as the pollination of native plants in key regions such as Sinaloa. According to Kunz et al. (2011), these roles represent complex ecological functions that urban bat communities fail to sustain.

Conversely, between the urbanized zones of Culiacán, our results suggest an almost complete exclusion of aerial and gleaning insectivore guilds in densely developed environments. Following the classification by Denzinger and Schnitzler (2013), the structural simplification of urban vegetation eliminates narrow-space and edge-space niches, critical habitats for species with limited maneuverability recorded at our sampling sites (*N. mexicanus*, *Myotis* spp., and *Pteronotus* spp.). Furthermore, these findings contrast with those from other northern Mexican cities, where species belonging to the families Molossidae and Vespertilionidae are also dominant (Rivera-Villanueva & Dalaí-López, 2023; Gutiérrez-Granados & Rodríguez-Zúñiga, 2024). Their absence in this urban sample suggests that local factors, such as fragmentation of riparian corridors and canopy discontinuity, act as severe physical barriers.

Additionally, anthropogenic sensory pollution plays a decisive role in environmental filtering. Artificial light at night (ALAN) in downtown Culiacán likely fragments the habitat of slow-flying, photophobic species such as *Myotis* spp. and *Pteronotus* spp., forcing them to use alternative routes to avoid predation (Stone et al., 2009; Gili et al., 2020, 2024). Similarly, anthropogenic noise can mask echolocation and social communication signals, displacing species that rely on passive listening for hunting (Lehrer et al., 2021). Nevertheless, the apparent absence of these families must be interpreted with caution due to sampling limitations. Mist nets inherently favor the capture of low-flying Phyllostomids, whereas aerial insectivores possess long-range echolocation systems that facilitate net evasion (MacSwiney G. et al., 2008). Therefore, this lack of records might partially reflect a methodological bias rather than a true local absence hypothesis, which should be corroborated in future studies by incorporating acoustic monitoring.

Ordination analysis (PCoA) and environmental vector fitting (envfit) identified urban cover as the primary driver of bat community structure ($R^2 = 0.99$, $p = 0.04$), which was greater than the effect of native

vegetation ($R^2 = 0.96$). This suggests that the intensity of urban infrastructure acts as the critical limiting factor for the local bat assemblage. However, a compelling pattern emerges when Ruzicka's dissimilarity at city edges is analyzed. The transitional sites, Cerritos and Primavera, exhibited equidistant dissimilarity relative to the control site, with values of 0.786 and 0.775, respectively.

Cerritos, which retain 48.8% of its native vegetation (tropical dry forest), may act as a qualitative refuge that preserves the taxonomic and functional identity of the original forest. The exclusive presence of *N. mexicanus* at this site is a finding of high conservation value. As a specialist in highly cluttered environments with strict microclimatic requirements (López-Wilchis et al., 2020), this species serves as a bioindicator of the still preserved structural integrity of peri-urban tropical dry forest patches. Its presence suggests that Cerritos acts as a critical “buffer zone” for species unable to adapt to the urban core.

In contrast, Primavera maintains quantitative similarity based on the biomass of tolerant species, which is supported by a matrix of managed vegetation and water bodies, but lacks the specialist taxa of the original site. This points to a replacement of specialization with generalization: while Cerritos loses absolute abundance but retains complex ecological functions, Primavera maintains biomass at the expense of functional simplification. Our results align with the dynamics described by Rodríguez-Segovia and Gaviláñez-Endara (2025), who caution that the loss of complex native vegetation eliminates trophic specialists, leaving communities dominated by species with broad environmental tolerances. According to these authors, this structural alteration increases niche overlap and wears down specialized interactions, explaining why highly managed sites such as Primavera can sustain bat biomass but fundamentally fail to replicate the ecological functionality of the original forest.

The functional evenness (FEve) did not decline linearly with urbanization; instead, it peaked at edge or transitional sites (Cerritos and Primavera). This finding aligns with patterns reported for fragmented Neotropical landscapes, where disturbed habitats (e.g., secondary forests) can exhibit greater functional evenness than primary forests (García-Morales et al., 2016). This suggests that following the environmental filtering of highly sensitive specialists generates a rearrangement of the bat assembly along peri-urban edges. This restructuring facilitates a more uniform distribution of abundances, driven by the persistence of taxa that efficiently exploit secondary vegetation. Species such as *S. parvidens* and *A. hirsutus*, which sustain substantial populations at sites such as Primavera, exemplify this ability to forage effectively within a heterogeneous matrix without being competitively displaced by the overwhelming dominance of *A. jamaicensis*.

Conversely, the drastic reduction in functional richness (FRic) and functional dispersion (FDis) within the urban core (Jardín Botánico) reflects severe environmental filtering. As noted by Ramírez-Mejía et al. (2020) across urban gradients in Colombia, the city acts as a selective filter that not only depletes species numbers but also erodes the diversity of life-history strategies, restricting persistence to a subset of taxa characterized by high mobility and trophic plasticity.

To transition toward a “bioinclusive city” model in Culiacán, we propose two key management strategies based on our findings and the current literature:

1. **Restoration of structural complexity:** Beyond merely increasing green cover, it is critical to emulate the native vertical stratification (understory and canopy) of the tropical dry forest within urban parks and gardens. This approach increases tree volume—a key predictor of diversity (Meramo et al., 2025), thereby creating accessible niches for narrow and edge space foraging guilds.
2. **Corridor connectivity:** The confluence of the Humaya, Tamazula, and Culiacán rivers provides an existing natural matrix to reconnect functional peripheral sites (Cerritos and Primavera) with the urban core. To be effective, however, these riparian corridors require continuous vegetation and the strict regulation of artificial light at night (ALAN) to facilitate the movement of photophobic species (Johnson et al., 2008; Lewanzik et al., 2022; Callas et al., 2024).

In conclusion, the urban development of Culiacán has generated a dichotomous landscape: an urban matrix numerically dominated by resilient species with high ecological plasticity and a fragmented periphery that likely still sustains the ecological function of the tropical dry forest. However, the high abundance of generalist bats within cities should not be misconstrued as an indicator of ecosystem health. Our findings are highly relevant, revealing the need for future conservation strategies that transcend demographic monitoring and incorporate population health assessments. It is crucial to recognize whether the urban environment genuinely functions as a high-quality refuge or, in fact, represents an ecological trap that causes overcrowding, compromising the long-term viability of these populations. Recognizing bats as complex bioindicators and managing the landscape by integrating structural vegetation complexity, riparian connectivity, and animal health will ultimately help transform the capital of Sinaloa into a model for sustainable urban ecosystems.

Declarations

Ethics approval

Animal handling and capture protocols were conducted in accordance with ethical guidelines and approved under the scientific collection permit SPARN/DGVS/10573/23 issued by the Dirección General de Vida Silvestre (DGVS) of the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT).

Competing Interests

The authors declare that they have no relevant financial or non-financial interests to disclose.

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Author Contribution

Conceptualization and study design: D.S.C.-C., A.L.-S., and J.D.J.-G.; Fieldwork and data collection: D.S.C.-C., A.L.-S., and J.D.J.-G.; Data analysis: D.S.C.-C., A.L.-S., J.J.Z.-A., and A.B.; Writing - original draft preparation: D.S.C.-C.; Writing - review and editing: A.L.-S., J.M.Z.-M., H.C.-U., E.H.T.-M., J.I.T.-A., and B.S.-M. All authors read and approved the final manuscript.

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Data Availability

The raw datasets supporting the conclusions of this article are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.19341439>

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Figures

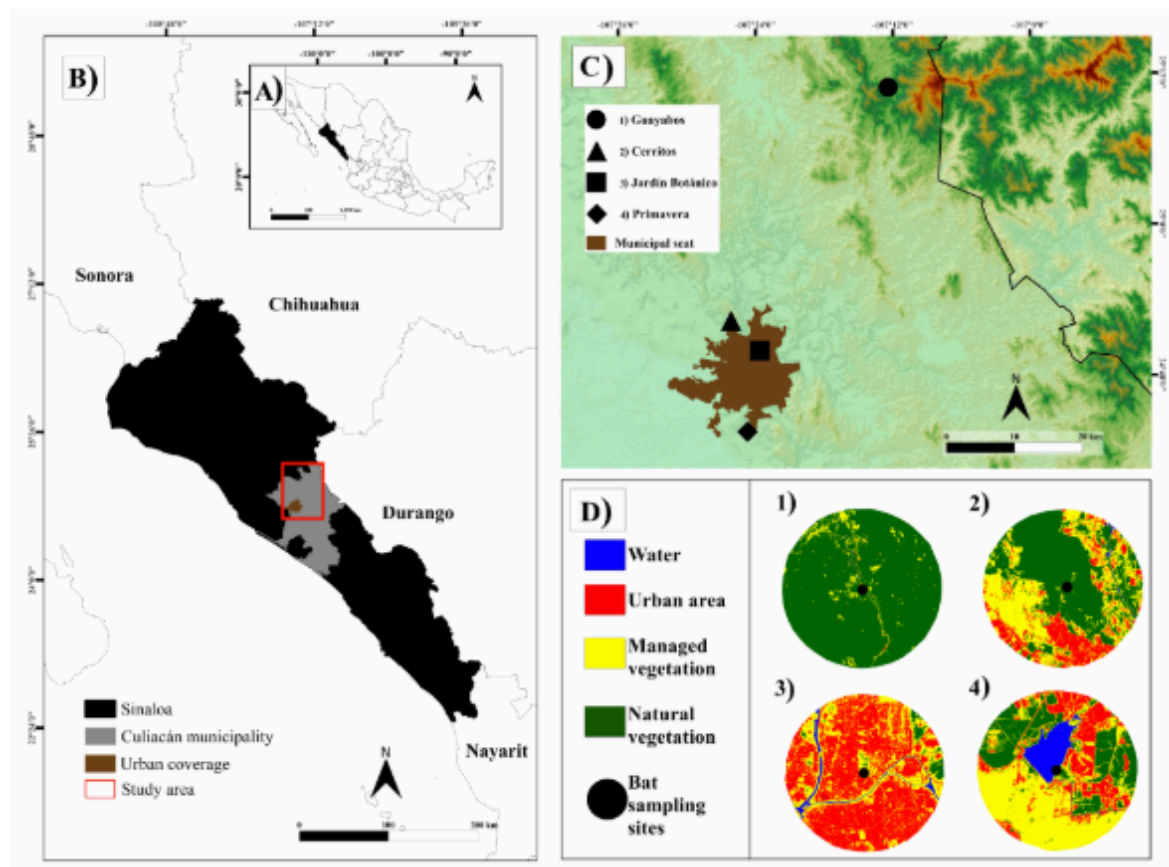


Figure 1

Geographic location and landscape characterization of the sampling sites.

Panels A and B show the municipality in the regional context of northwestern Mexico. Panel C details the spatial distribution of the sites: 1) Guayabos (control), 2) Cerritos (forest transition), 3) Jardín Botánico (urban), and 4) Primavera (agricultural transition). Panel D illustrates the landscape composition within a 3-km radius buffer for each site, categorizing land cover into water (blue), urban area (red), managed vegetation (yellow), and native vegetation (green).

Alt text: A multi-panel map illustrating the geographic location of the Culiacán municipality in northwestern Mexico, alongside the spatial distribution of four bat sampling sites: Guayabos, Cerritos, Jardín Botánico, and Primavera. Four circular buffer charts display the contrasting land cover proportions —water, urban area, managed vegetation, and natural vegetation—within a 3kilometer radius of each specific site.

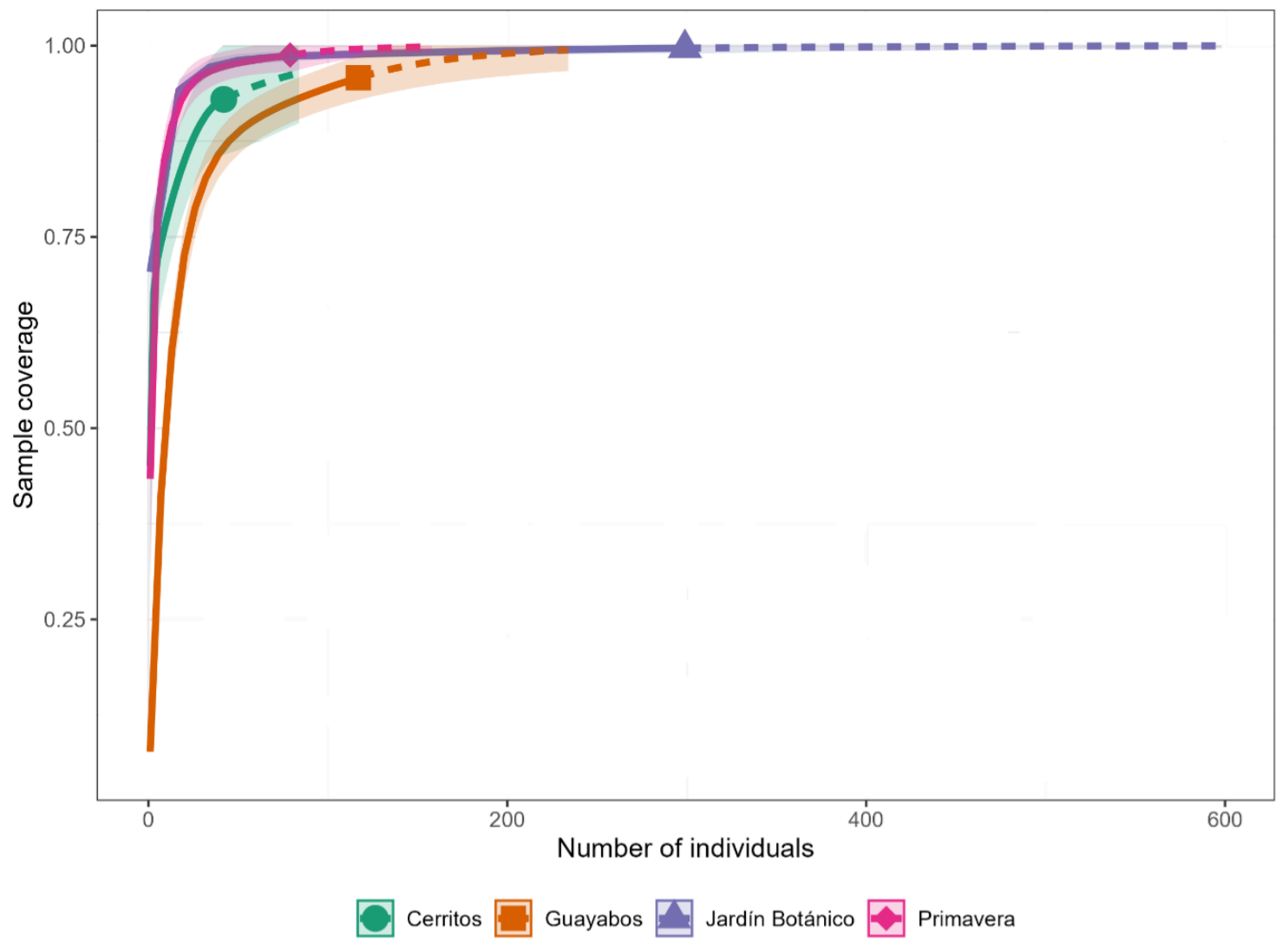


Figure 2

Inventory completeness curves for the four study sites.

The solid and dashed lines represent rarefaction and extrapolation, respectively, with their 95% confidence intervals (shaded areas). The markers indicate the observed abundance. The y-axis expresses sample coverage as a proportion (0–1).

Alt text: A line graph displaying sample coverage curves for bat inventories at four study sites. The x-axis represents the number of individuals, and the y-axis represents sample coverage as a proportion from 0 to 1.0. All four curves rise steeply and plateau above 0.90, visually confirming high inventory completeness across all locations.

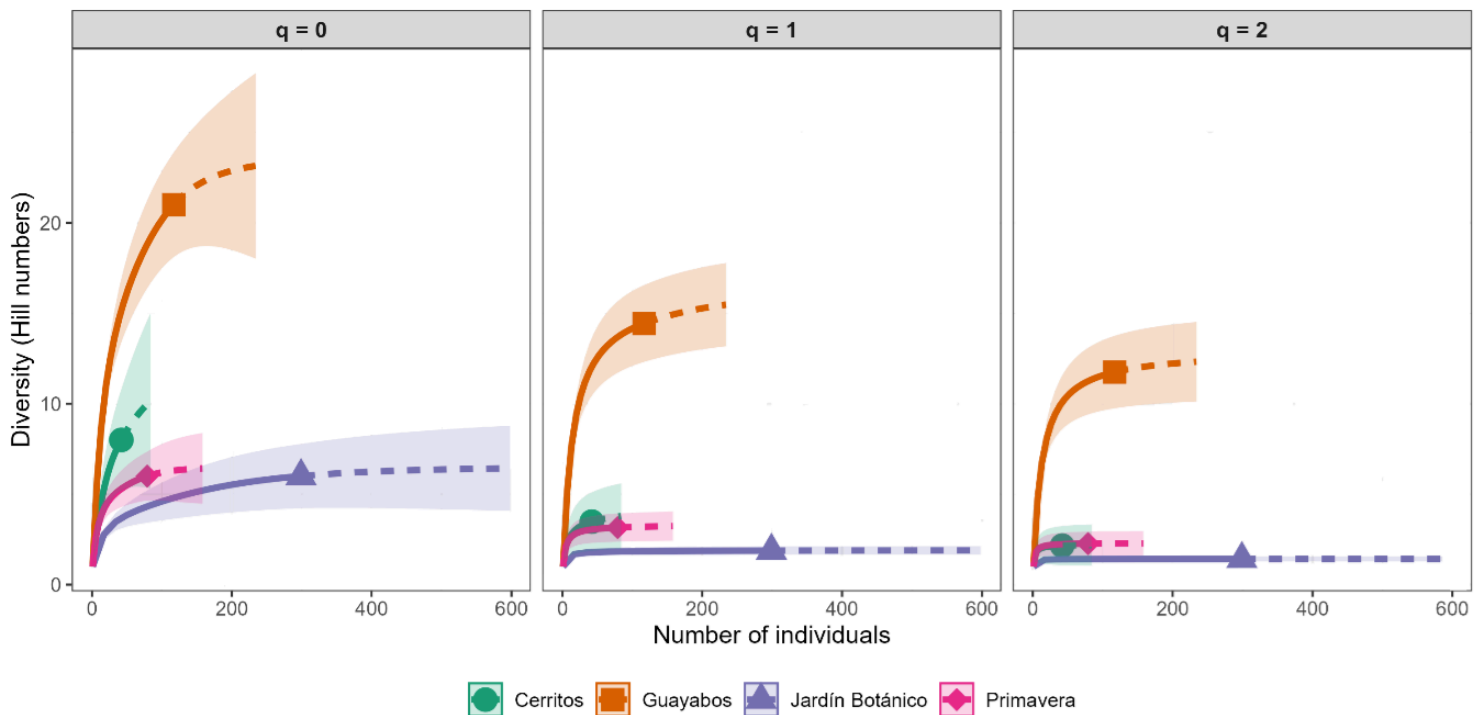


Figure 3

Diversity profiles of bat assemblages across three q orders based on Hill numbers.

Species richness ($q = 0$), Shannon diversity or common species ($q = 1$), and Simpson diversity or dominant species ($q = 2$). The solid and dashed lines represent the rarefaction and extrapolation curves, respectively. The shaded areas indicate 95% confidence intervals (50 bootstrap replications). Nonoverlapping confidence intervals indicate significant differences at the $\alpha = 0.05$ level.

Alt text: A set of three line graphs showing bat diversity profiles based on Hill numbers for q equals 0, 1, and 2. The y-axis represents diversity and the x-axis represents the number of individuals. The curves demonstrate the Guayabos site maintains the highest diversity across all three panels, while the Jardín Botánico site exhibits the lowest diversity.

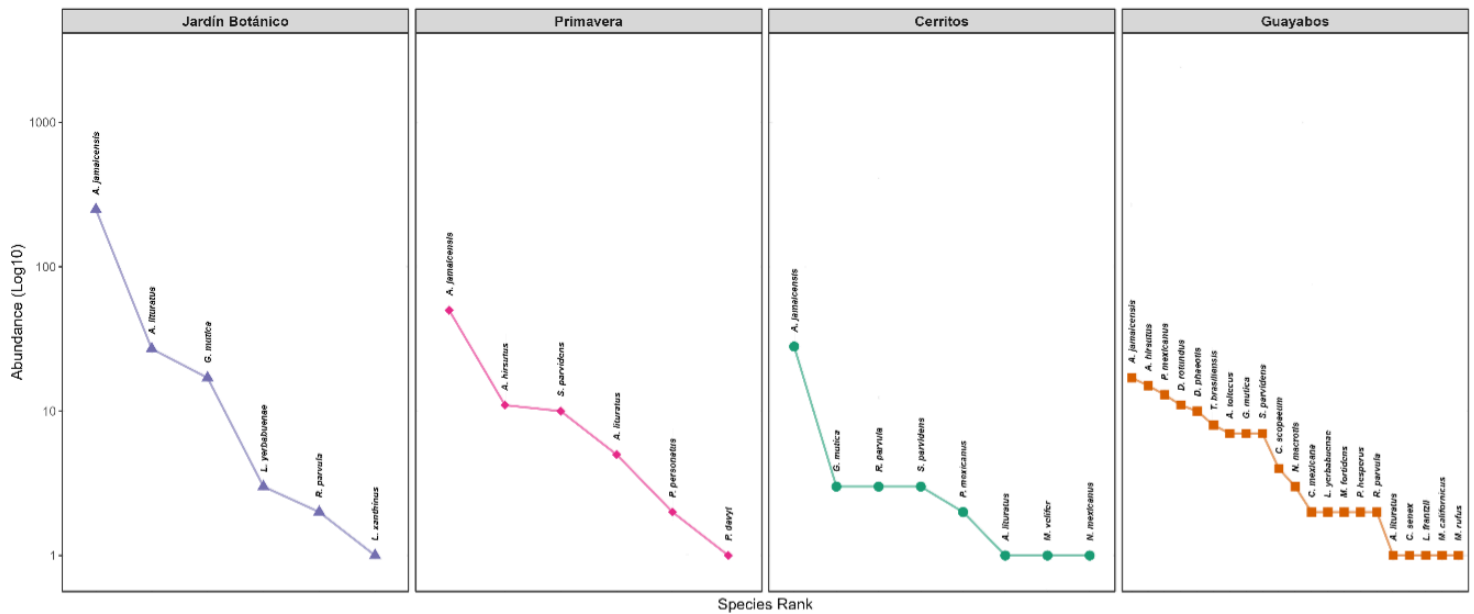


Figure 4

Rank-abundance (Whittaker) curves of bat species across the four sites along the urbanization gradient.

Sites are ordered from the highest to the lowest degrees of urbanization. The y-axis displays absolute abundance on a logarithmic scale ($\log_{10}$), whereas the x-axis ranks species from most abundant (rank 1) to least abundant. The steep slope at the urban sites indicates high dominance and low evenness, which contrasts with the shallow slope observed in the conserved site.

Alt text: Four separate line graphs displaying rank-abundance Whittaker curves for each study site. The y-axis show species abundance on a logarithmic scale, and the x-axis shows species rank. The panels for the Jardín Botánico and Primavera site feature steep downward slopes indicating high dominance of a single species, contrasting with the shallower slope of the Guayabos site which indicates greater species evenness.

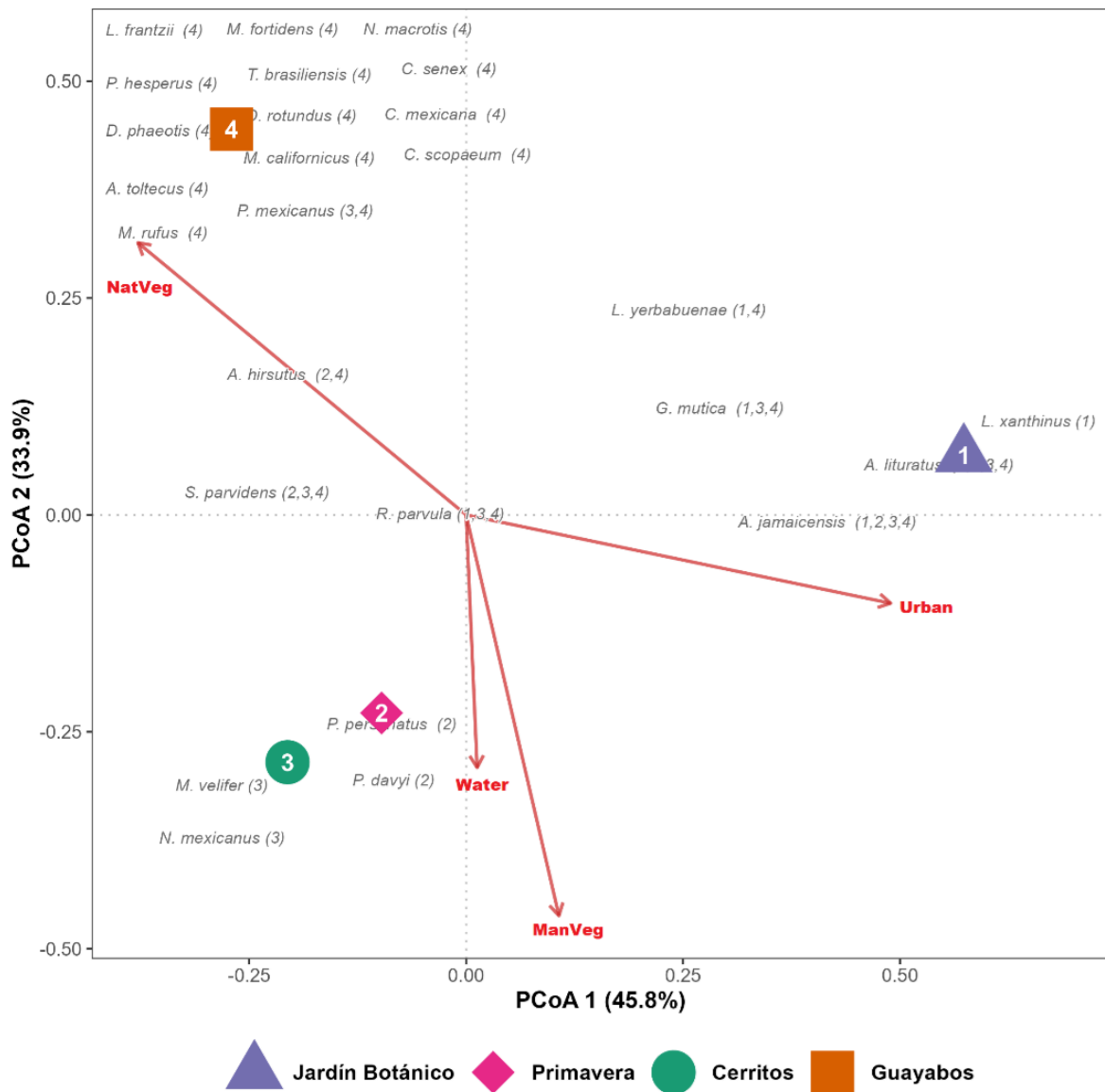


Figure 5

Ordination of bat assemblages via principal coordinate analysis (PCoA) based on Ruzicka dissimilarity.

The colored points represent the study sites. The gray text indicates the location of the species in the multivariate space (centroids); the numbers in parentheses indicate the sites where each species was present. Red arrows show the projection of fitted landscape variables (envfit function), representing the percentage cover of each land use; the direction of the arrow indicates the gradient of increasing coverage. Urban (urban cover), NatVeg (native vegetation), ManVeg (managed vegetation), and water (water bodies).

Alt text: A scatter plot illustrating a Principal Coordinate Analysis of bat assemblages across the four study sites. The horizontal and vertical axes represent the percentage of variance explained. Red vectors represents environmental drivers, showing the urban cover arrow pointing strongly towards the Jardín Botánico site, while native vegetation arrow points in the opposite direction.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryData.docx](#)