THERYA, 2025, Vol. 16(3):335-350 DOI:10.12933/therya-25-6197 ISSN 2007-3364

Distribution, ecology, and natural history of the Spectral bat (*Vampyrum spectrum*) in Colombia

Tatiana Velásquez-Roa[1,6*], Christian Cabrera-Ojeda[2,3,4], Andrea Bernal-Rivera[5,6], Cristian Calvache-Sánchez[6], Pamela Carvajal-Nieto[6], Sara Medina-Benavides[7], and Jonathan Granobles-Cardona[8]

[1]Biology Department, Texas State University. 601 University Dr., 78666, San Marcos; Texas, USA. (TVR)
[2]Grupo de Investigación en Ecología Animal, Universidad del Valle, Ciudad Universitaria Meléndez, Calle 13 # 100-00, Cali; Valle, Colombia.
[3]Asociación GAICA, Barrio San Ignacio, Nariño, Colombia.
[4]Grupo de investigación en Ecología Evolutiva, Universidad de Nariño, Nariño, Colombia. Email: cabrera.christian@correounivalle.edu.co (CCO)
[5]Calima, Fundación para la Investigación de la Biodiversidad y Conservación en el Trópico, Cali; Valle, Colombia. Email: bernalriverandrea@gmail.com (ABR)
[6]Departamento de Biología, Universidad del Valle, Ciudad Universitaria Meléndez, Calle 13 # 100-00, Cali; Valle, Colombia. Email: cristian.calvache@correounivalle.edu.co (CCC), pamelacarvani@gmail.com (PCN)
[7]Laboratório de Ecologia Evolutiva, Universidade Estadual de Montes Claros. Montes Claros, Brazil. Email: medina.sara@correounivalle.edu.co, (SMB)
[8]Grupo de investigación en recursos filogenéticos, Universidad Nacional de Colombia, Ave Cra 30 #45-3, Bogotá; D.C., Colombia. Email: granobles@unal.edu.co, (JGC)
[*]Corresponding author: yxh11@txstate.edu (TVR)

Species distribution and ecology are heavily influenced by ecosystem structure and dynamics, where shifts in land use and habitat loss jeopardize the survival of populations. This is especially important for top predators, such as Spectral bat (*Vampyrum spectrum),* which is thought to depend on conserved areas with large resource availability. It is the largest bat in the Americas. Here, we report the second record of the Spectral bat for Valle del Cauca, Colombia, and the first record for the region's Tropical Dry Forest. We also report key morphological and ecological information associated to a couple individuals from Colombia's Pacific region. Further, we analyzed the association of the Spectral bat's presence in Colombia with biome, ecosystem, and vegetation cover type. Historical distribution analysis shows a decrease in stable forest areas ranging from 1990 to 2017. Most *V. spectrum* records are from the Andean region, with significant associations of biomes and vegetation cover. Surprisingly, the areas where the species has been recorded in the last years correspond to a mix of forests, urban areas and agricultural lands. The diet of the carnivore Spectral bat includes 12 vertebrate species, predominantly rodents and birds, while sugar assimilation seems to be low and slow, as expected for its protein rich meal consumption with low sugar content. This study contributes to the understanding of *V. spectrum's* ecological needs and highlights critical areas for future research and conservation efforts to ensure the species' survival in Colombia.

Key words: Bats, diet, forest and non-forest, habitat, top predator.

La distribución y la ecología de las especies están influidas por la estructura y la dinámica de los ecosistemas, donde los cambios en el uso del suelo y la pérdida de hábitat ponen en peligro la supervivencia de las poblaciones. Esto es especialmente importante para los depredadores tope, como el murciélago espectral (*Vampyrum spectrum*), que se cree que depende de zonas conservadas con gran disponibilidad de recursos. El murciélago espectral es el murciélago más grande que se encuentra en el continente americano. Aquí, reportamos el segundo registro del murciélago espectral para el Valle del Cauca, Colombia, y el primer registro para el Bosque Seco Tropical de la región. También reportamos información morfológica y ecológica clave asociada a un par de individuos de la región Pacífica de Colombia. Además, analizamos la asociación de la presencia del murciélago espectral con biomas, ecosistemas y tipo de cobertura vegetal presentes en Colombia. El análisis de la distribución histórica muestra una disminución en las áreas de bosque estable entre 1990 y 2017. La mayoría de los registros de *V. spectrum* proceden de la región andina, con asociaciones significativas a biomas y cobertura vegetal. Sorprendentemente, las zonas donde se ha registrado la especie en los últimos años corresponden a una mezcla de bosques, zonas urbanas y tierras agrícolas. La dieta del murciélago espectral carnívoro incluye 12 especies de vertebrados, predominantemente roedores y aves, mientras que la asimilación de azúcares parece ser baja y lenta, como era de esperar por su consumo de comidas ricas en proteínas con bajo contenido en azúcares. Este estudio contribuye a la comprensión de las necesidades ecológicas de *V. spectrum* y destaca áreas críticas para futuras investigaciones y esfuerzos de conservación para asegurar la supervivencia de la especie en Colombia.

Palabras clave: Bosque/no bosque, dieta, hábitat, murciélagos, depredador tope.

The spatial distribution of species is strongly influenced by the structure and dynamics of the ecosystems in which they inhabit (Gaston 2003). Bats are highly sensitive to changes in land cover and ecosystem transformation (Meyer *et al.* 2016). The Spectral bat (*Vampyrum spectrum*) is recognized as the largest carnivore bat species present in the New World (Altringham 2011). It is currently classified as Near Threatened (NT) by the International Union for Conservation of Nature (Solari 2018). It is associated with a variety of habitats that provide shelter and food resources, from tropical rainforests to transitional ecosystems (Emmons and Feer 1997). However, changes in land-use patterns and loss of natural ecosystems can significantly affect the distribution and survival of this species (Simmons and Voss 1998).

The Spectral bat, which ranges from southern Mexico to Bolivia and across the Amazon Basin, is considered rare due to low abundance and limited records (Greenhall 1968; Sousa *et al.* 2016; Acosta *et al.* 2019; Pacheco-Figueroa *et al.* 2022). It is thought to prefer conserved forested areas, where it functions as a top predator, preying on birds, rodents, and other bats (Vehrencamp *et al.* 1977; Gardner 2008; Solari 2018). Despite its ecological significance, aspects of its ecology and population dynamics remain largely unknown. In Colombia, it inhabits various ecosystems across all biogeographic regions (Esquivel *et al.* 2020), but the few records hinder understanding of its population status and local distribution. Existing reports indicate a declining population trend, reflecting its rarity despite widespread range (Reid 2009; Solari 2018).

Because of its poorly documented history in Colombia, it has not been included in any risk assessments in the past (Rodríguez-Mahecha *et al.* 2006) nor in the most recent assessment of wildlife endangered species of Colombia (Resolución 0126 de 2024 by MADS 2024). Many aspects of natural history, population ecology and current distribution of *Vampyrum spectrum* are still unknown in the country, having just 38 valid records in a frame of approximately 80 years (1942 to 2023) (Rivas-Pava *et al.* 2007; Pinto-Orozco *et al.* 2023) out of 344 records on its distributional range (GBIF 2023) which limits the assessment of its conservation status. Overall, studies have been focused in understanding *V. spectrum*'s diet (Gardner 1977; Navarro and Wilson 1982; Gardner 2008), others have provided information about its movement and echolocation (Martínez-Fonseca *et al.* 2022), home range (Vehrencamp *et al.* 1977, Sousa *et al.* 2016), its local distribution (Esquivel and Rodríguez-Bolaños 2018; Pinto-Orozco *et al.* 2023), and biogeographic affinity (Esquivel *et al.* 2020), being the latter the most comprehensive approximation for Colombia. In Valle del Cauca, a department located in the Pacific region of Colombia, the first record of the species was recent; it was reported in a small fragment of premontane humid forest in the Bosque de Yotoco Natural Reserve (Pinto-Orozco *et al.* 2023), confirming its presence in this region in the southwestern part of the country.

However, none of the mentioned studies have tested the habitat affinity of the Spectral bat, a key aspect to understand and predict the species response to habitat changes (López-Bosch *et al.* 2022). The relationship between changes in land cover and biome structure provides a comprehensive perspective on habitat requirements of *Vampyrum spectrum*, especially in humid tropical and mountain biomes, as well as in transitional ecosystems between primary and secondary forests (Sierra *et al.* 2007). Studying the distribution of the species in relation to changes in cover and biome structure can lead to the identification of habitat displacement trends and the impact of fragmentation (Laurance *et al.* 2014), which provides valuable information for conservation strategies at the national level. Hence, our aim was to determine, for the first time, the association between *Vampyrum spectrum* records and: 1) biomes, 2) ecosystems, and 3) vegetation covers in Colombia. We hypothesized that *V. spectrum* would show a stronger association with vegetation cover, and therefore a higher number of records in well-conserved areas. Furthermore, we present ecological and morphological data and report the first record of the species within the highly fragmented Tropical Dry Forest of Valle del Cauca, Colombia. Additionally, our Bayesian model indicates that the variation in the number of *V. spectrum* records is best explained by the nested structure of Biome, Ecosystem, and Cover; suggesting that ecological context at multiple spatial scales plays a significant role in shaping distribution patterns. This information is essential for species conservation, particularly considering the rapid transformation of forested areas in the Neotropics.

Materials and methods

Our study area included 10 remnants of Tropical Dry Forest (TDF) of Valle del Cauca, Colombia from 2019 to 2021 (Velásquez-Roa and Calvache-Sánchez 2021). TDF is characterized to present a bimodal regimen climate, with rainy seasons between April – May and October – November, which represents 70% of annual precipitation, and two dry seasons between January – February and July – August (Armbrecht and Ulloa-Chacón 1999). The average altitude of the places visited was 1050 m above sea level. These remnants are characterized by a high intervention rate, logging, and the presence of *Chusquea* spp. The new record in Colombia for Spectral bat was captured at Hacienda La Venta, which is a private area in the municipality of Bugalagrande, Valle del Cauca. It is part of the basin of Paila river and Cauca's River hydrographic region (Figure 1). This area is dominated by grass used for livestock and 120 ha of TDF. The individual was captured under the collect permit 100 No. 1122 of October 23, 2018, given to the project "Contribución a la conservación del Bosque Seco Tropical del Valle del Cauca a través del fortalecimiento Valle del Cauca occidente" and deposited at the Colección Zoológica de referencia científica, INCIVA (IMCN 165). Seven dominant plant species at the Hacienda La Venta were *Croton schiedeanus, Aniba perutilis, Zanthoxylum rhoifolium, Miconia spicellata, Machaerium capote, Clarisia biflora* and *Nectandra* sp., all of them with thin stem and height between three m to 20 m, which is indication of a highly modified environment.

Historical distribution and ecological affinity. To evaluate habitat changes in areas where *Vampyrum spectrum* has been recorded in Colombia, we compiled occurrence data from Esquivel *et al.* (2020) and Pinto-Orozco *et al.* (2023) along with the new record reported in this study, totaling 39 occurrences (N=39) and we compiled a forest and non-forest map from IDEAM (2019) between 1990 and 2017

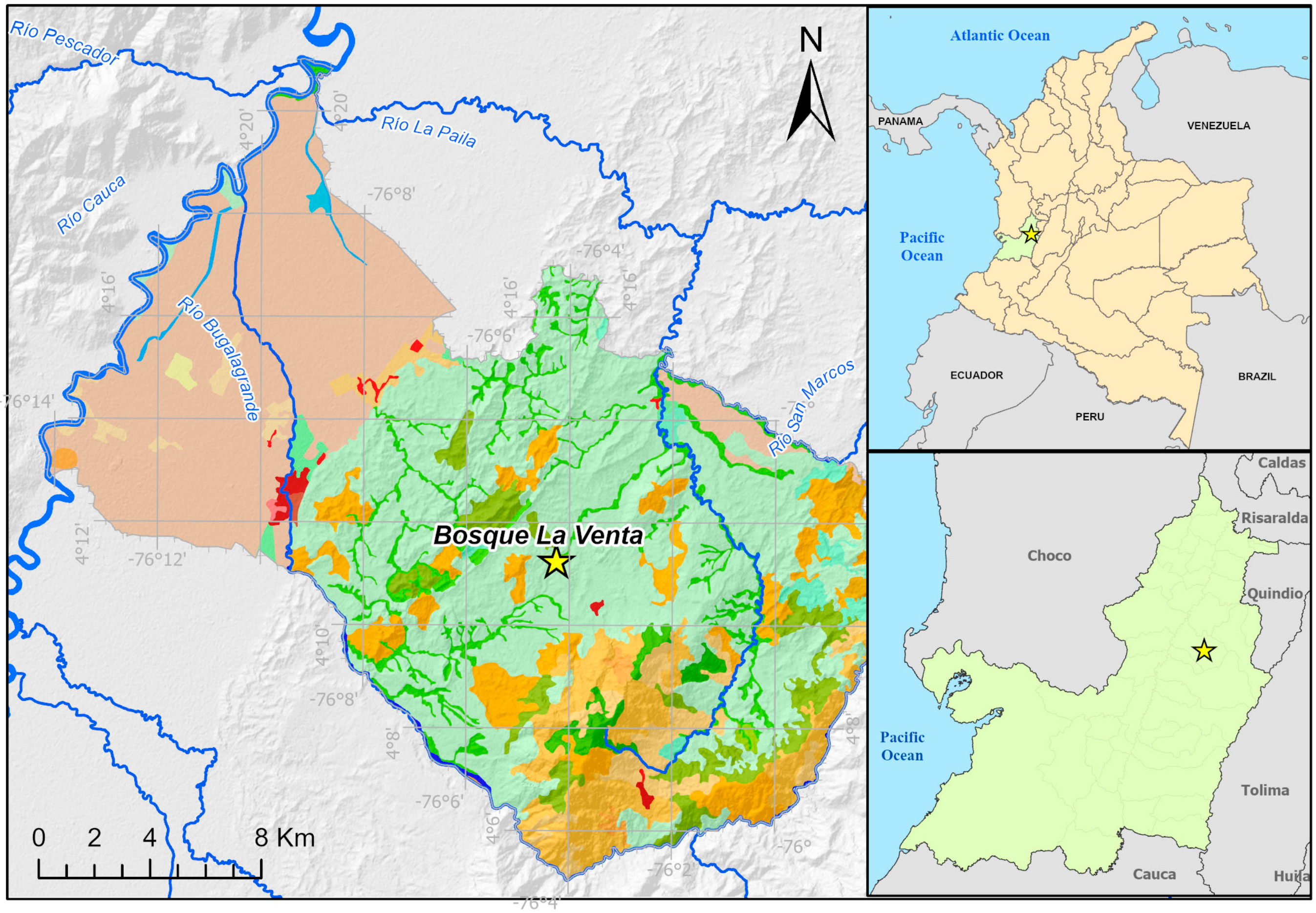

Figure 1. Vegetation covers of the habitat where *Vampyrum spectrum* was captured during the current study; Hacienda La Venta, Bugalagrande, Valle del Cauca, Colombia ( ). Sources: IDEAM: Coverages 2020, CVC: Basic cartographic 2021, IGAC: Basic cartographic 2019. Light green areas: secondary forest.

(~30 m). IDEAM classifies habitat changes into five classes: stable forest, non-stable forest, deforestation, regeneration, and areas with no available information. Furthermore, we incorporated the terrestrial, marine, and coastal ecosystem map and the biome classification by the Instituto Humboldt (1:100.000, IDEAM *et al.* 2017), which classifies Colombian ecosystems based on ecological and structural attributes. These resources are essential for assessing deforestation, regeneration, and forest stability, providing key insights into the spatial dynamics of the species. Furthermore, we quantified the extent of area loss by comparing the forest and non-forest raster data from 2017 with that from 1990, calculating the difference to identify areas of change over time. To categorize the magnitude of vegetation loss, we applied a threshold-based classification using the following criteria: significant loss (³ 30% decrease), moderate loss (10.1% to 29.9% decrease) and minor loss (0.1% to 10% decrease). These thresholds were implemented using conditional logic in the Raster Calculator tool in ArcGIS Pro 3.4.0 (ESRI 2024). The resulting classified raster was then used to calculate the total area of loss per category by multiplying the number of pixels in each class by the area of a single pixel (900 m^2). The results were expressed in square kilometers and as percentages of the total affected area.

To examine associations between biome, ecosystem, and vegetation cover in relation to Spectral bat records, we applied a randomization test to account for the small sample size, followed by a Chi-square test at a significance level of 0.05, as an exploratory analysis. Additionally, due to the small sample size, we employed a Bayesian approach, fitting a hierarchical model with nested random intercepts to evaluate whether the nested structure of Biome, Ecosystem, and Cover explained the variation in bat records (counts) in Colombia. We fitted a Poisson bayes model using the brm function from the brms package (Bürkner 2021) with 3 chains, 30000 iterations, 10000 warmup and thin equal 1. We defined our priors as normal (0, 1) for the intercept (assumes the log of expected counts is centered around 0 with moderate uncertainty) and exponential (1) for random effect standard deviations (encourages smaller group-level variation unless strongly supported by the data). The analyses were conducted in R software version 2024.12.0+467 (R Core Team 2024).

Morphology. We took external and craniodental measurements of the specimen captured at Hacienda La Venta. Additionally, to increase the available morphological

Figure 2. Cranioventral, lateral and dorsal views of the *Vampyrum spectrum* specimen's cranium and dorsal view of specimens' skin (IMCN 165) collected in Hacienda La Venta, Bugalagrande, Valle del Cauca, Colombia.

information of the species from the Pacific region of Colombia we also visited two mammal collections. We report measurements of a specimen deposited in the Colección Zoológica at Universidad de Nariño (PSO-Z MUN 663 and its neonate MUN 663B) and two specimens deposited in the Colección de Mamíferos at Universidad del Valle (UV-13281, UV-13282) that have not been previously published (Figure 2). Following Simmons and Voss (1998), standard external (n = 3) and craniodental (n = 13) measurements were taken using digital calipers of 0.01 mm accuracy. For all the individuals, the external measures were hind foot length (HF), ear length (E) and forearm length (FA), while the craniodental measures were: Greatest length of the skull (GLS), Condyloincisive length (CIL), Condylocanine length (CCL), Zygomatic breadth (ZB), Maxillary toothrow length (MTRL), Mandibular toothrow length (MANDL), Postorbital breadth (PB), Braincase breadth (BB), Braincase height (BH) without the sagittal crest, Palatal length (PL), Canine-Canine breadth (C-C), Superior Canine length (SCL) and Inferior Canine length (ICL) both considered in teeth without wear.

Diet. Diet information from the individual caught at Hacienda La Venta was not possible to identify (feathers); however, we compiled diet information from an individual captured in El Algodonal village, municipality of Taminango, department of Nariño by one of this study's authors (October 2013). The specimen was caught in a shallow cavern of 30 m (5x7) above the south bank of the Mayo River. The cave was inhabited by a group of four adult Spectral bats, one of which was a female with a neonate, collected and deposited at Colección Zoológica Universidad de Nariño (PSO-Z) (MUN 663 – MUN 663B). Approximately 1 kg of biological material

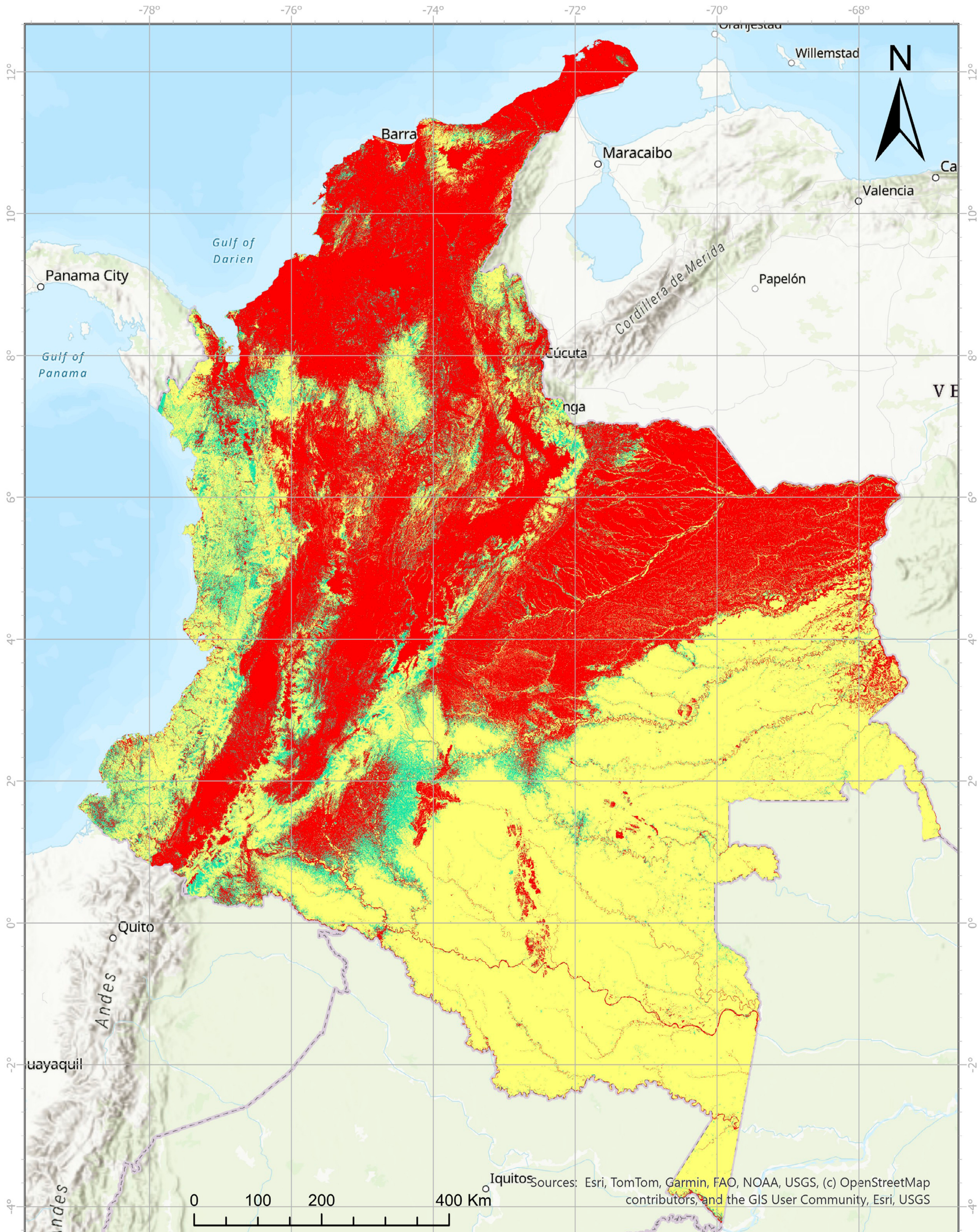

Figure 3. Categorization of vegetation loss in Colombia (1990–2017) based on a 30% reduction threshold derived from forest and non-forest cover data (IDEAM 2019). The map indicates areas of high vegetation loss (red), moderate vegetation loss (green), and minor vegetation loss (yellow) in Colombia.

Table 1. Standard external and craniodental measurements in millimeters (mm) for four adult specimens and a neonate of *Vampyrum spectrum. The mean (x̄), standard deviation (sd) and sex are provided only for adult specimens.* These specimens are housed in the Colección Zoológica de Referencia INCIVA (IMCN), the Colección de Mamíferos at Universidad del Valle (UV), and the Colección Zoológica at Universidad de Nariño (PSO-Z), respectively. *Cranial measurements are not included.

	INCIVA (This study) IMCN	**Universidad del Valle**		**Universidad de Nariño**		**x̄ ± sd**
		UV		**PSO-Z**		**Adult specimens**
Measurements	IMCN-165	UV-13281	UV-13282	MUN-663	MUN-663B	
(mm)	♀	♀	♂	♀	Neonate*	
E	43.49	37.37	39.03	38.80	19.40	39.67 ± 2.65
HF	27.67	19.16	25.78	28.40	25.65	25.25± 4.21
FA	109.09	96.98	103.55	106.40	41.15	104.01 ± 5.20
TL	146.56	138.73	113.74	147.71	58.48	136.69 ± 15.81
GLS	53.26	50.43	51.00	52.49		51.80 ± 1.31
CIL	44.37	42.24	43.73	43.82		43.54 ± 0.91
CCL	44.51	42.10	43.22	43.34		43.29 ± 0.99
ZB	24.45	22.75	24.25	23.52		23.74 ± 0.77
MTRL	21.14	19.78	20.85	21.28		20.76 ± 0.68
MANDL	22.95	21.96	23.05	23.32		22.82 ± 0.59
PB	8.31	7.48	8.15	8.14		8.02 ± 0.37
BB	16.58	15.32	16.4	15.99		16.07 ± 0.56
BH	18.01	15.51	18.32	17.99		17.46 ± 1.31
PL	20.18	19.70	21.41	21.29		20.65 ± 0.84
C-C	8.37	8.17	9.38	9.22		8.79 ± 0.60
SCL	8.03	7.19	8.06	7.49		7.69 ± 0.43
ICL	8.08	6.71	8.72	7.8		7.83 ± 0.84
Weight	158	120	-	>250		

Conventions

External: E: ear length, HF: Hind foot length, FA: Forearm, TL: Total length

Cranial: Greatest length of the skull (GLS), Condyloincisive length (CIL), Condylocanine length (CCL), Zygomatic breadth (ZB), Maxillary toothrow length (MTRL), Mandibular toothrow length (MANDL), Postorbital breadth (PB), Braincase breadth (BB), Braincase height (BH) without the sagittal crest, Palatal length (PL), Canine-Canine breadth (C-C), Superior Canine length (SCL) and Inferior Canine length (ICL) both considered in teeth without wear.

found at the bottom of the roosting site was collected. The material was separated into identifiable/non-identifiable components and separated into items by morphological similarity. The birds' feathers and skulls recovered were compared with specimens housed at the PSO-Z and the Colección de Mamíferos of Universidad del Valle (UV) to determine the lowest taxonomic level possible for the preys. This information was simultaneously contrasted with information on the species list of the sampled locality.

Sugar assimilation. We measured glucose assimilation in the individual caught at Hacienda La Venta, Bugalagrande, Valle del Cauca (2020). After a 10-hour fasting period, we measured blood glucose levels using a glucometer GlucoQuick G30a (Diabetrics®). We extracted a blood drop from the forearm using a lancet and the measurement was directly done through the meter strips. Subsequently, we fed the bat with a 20% glucose solution 5.4 g/kg body weight based on Kelm *et al.* (2011). Then we measured blood glucose levels 10, 30 and 60 minutes after the glucose ingestion to build a glucose tolerance curve. The essays were conducted ensuring the welfare of the animal during sample collection according to the guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes and ACUC 2016), and the physiological study was conducted under the permit of the National Authority of Environmental licenses and the Ministry of Environment and Sustainable Development of Colombia, Resolution 1070, 28 August 2015.

Results

During the fieldwork at Hacienda La Venta, an adult post-lactating female *V. spectrum* was captured using ground mist nets in August 2020. The exact location where the individual was caught was an edge between a secondary forest and a grassland (Figure 1). This represents the second confirmed record for Valle del Cauca and the first for the very fragmented and diminished Tropical dry forest in the department. Morphometrics for our specimen (IMCN -165) are presented in Table 1, along with previously unpublished data for specimens housed at the Colección de Mamíferos

Table 2. Summary of results from the hierarchical Bayesian model with nested random effects. The model includes random intercepts for Biome, Ecosystem (nested within Biome), and Cover (nested within Ecosystem and Biome). Estimates are presented alongside their lower (l-95% CI) and upper (u-95% CI) 95% credible intervals, standard deviation (sd), standard error (Est.error), convergence diagnostics (Rhat) and effective sample sizes (Bulk_ESS and Tail_ESS). Parameters whose credible intervals do not include zero are considered to have a statistically significant effect (bold numbers).

Multilevel	**Hyperparameters:**						
~Biome	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.37	0.31	**0.01**	**1.14**	1	22265	24533
~Biome:Ecosystem							
sd(Intercept)	0.3	0.22	**0.01**	**0.8**	1	21533	24274
~Biome:Ecosystem:Cover							
sd(Intercept)	0.29	0.22	**0.01**	**0.8**	1	21887	24872
Regression	**Coefficients:**						
Intercept	0.56	0.3	-0.09	1.1	1	35548	32093

Draws were sampled using sampling (NUTS). For each parameter, Bulk_ESS and Tail_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

of Universidad del Valle (UV-13281, UV-13282) and Universidad de Nariño (MUN-663, MUN-663B).

Historical distribution and ecological affinity. To assess changes in the forest cover and geographical distribution of *V. spectrum* in Colombia (in forest and non-forest areas), we analyzed habitat transformations over time. Between 1990 – 2017, stable forest areas showed a marked decline, with notable losses in the Pacific, Andean and Amazon regions. Similarly, areas classified as "no information", were predominant between 1990 and 2010. Deforestation was consistently present from 1990 to 2012. The category of regeneration, in contrast, was minimally represented due to its localized nature, making it difficult to visualize at a broader scale. Non-stable forests, which dominate most of the national territory, are associated with regions experiencing higher levels of anthropogenic activity. Most *V. spectrum* records have been reported in the Andean region, followed by the Pacific, Orinoquia, Amazon and, to a lesser extent, the Caribbean region. To further quantify these changes, we applied a 30% decrease threshold to classify the severity of loss. This analysis revealed that approximately 468,168 km^2 experienced a significant loss (43%), 100,130 km2 underwent a moderate loss (9%) and 533.514 km2 experienced a minor loss (48%) (Figure 3, Table 3).

Table 3. Area and proportion of vegetation loss categories in Colombia (1990–2017) based on 30% decreased threshold. Area values were calculated by multiplying the pixel count by 0.0009 km^2, due to spatial resolution of 30 meters per pixel.

Category	Pixel count	Area (Km^2)	Percentage total loss
Significant loss (^{3} 30%)	520205048	468,168.54	42.49%
Moderate loss (10.1% to 29.9%)	111255970	100,130.37	9.09%
Minor loss (0.1% to 10%)	592793639	533,514.28	48.42%

Statistical analysis revealed a significant association between *V. spectrum* records and biome type (X2 = 18.8, p value = 0.001) as well as vegetation cover (X2 = 13.6, p value = 0.04) but not significant association with ecosystem type (X2 = 7.3, p value = 0.21) (Figure 4A). Many records were located within the Tropical Humid Zonobiome (ZHT) and were associated with the grasslands (PA) and mosaics vegetation cover types (MO) (Figure 4B, 4C). On the other hand, the posterior estimates obtained through the Bayesian model revealed that the variation in bat counts is meaningfully structured across all three spatial levels (Table 2). The standard deviations of the random intercepts were Biome: 0.37 (95% CI: 0.01–1.14), Ecosystem within Biome: 0.30 (95% CI: 0.01–0.80) and Cover within Ecosystem and Biome: 0.29 (95% CI: 0.01–0.80) (Figure 5). These estimates suggest that each level of the ecological hierarchy contributes to explaining the variability in *V. spectrum* records, with no single level dominating the structure. All model diagnostics indicated good convergence ($\hat{R}$ = 1.00) and high effective sample sizes, supporting the reliability of the posterior estimates (Table 2). These results underscore the importance of accounting for multi-scale ecological structure when modeling species distribution data, especially in complex landscapes like those found in Colombia. Analysis of present-day vegetation cover (IDEAM *et al.* 2017) in areas where *Vampyrum spectrum* has been recorded indicates that the species primarily occupies highly heterogeneous landscapes. Notably, only five out of 39 records correspond to dense forest areas, while nearly half are in proximity to urban developments or agricultural zones, suggesting a degree of adaptability to modified environments.

Diet and sugar assimilation. We recorded 12 vertebrate species in the diet of the Spectral bat, where four species were mammals, and eight were birds. In the case of mammals, we found a total of 41 skulls of rodents (Cricetidae) where 63.4% corresponded to *Zygodontomys brunneus* (26)

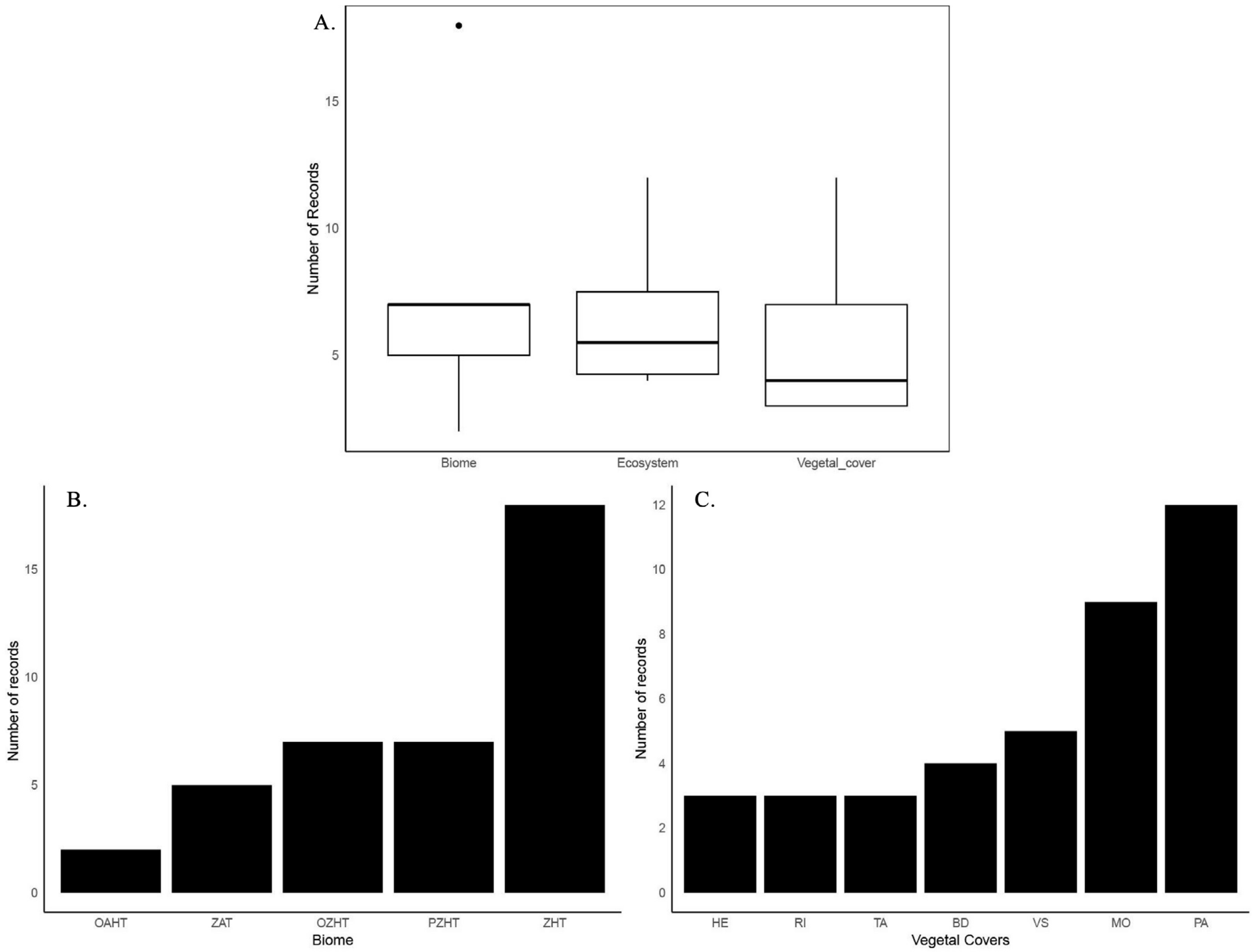

Figure 4. Visual representation– Boxplot – of the distribution of the number of records of *Vampyrum spectrum* per biome, ecosystem and vegetal cover (A). Comparison of number of records of *V. spectrum* by biome (B) and by vegetal covers (C). For acronyms see IDEAM et al. (2017).

and 21.95% corresponded to *Reithrodontomys mexicanus* (9). Additionally, we found two bat species, *Phyllostomus discolor* (n=2; Phyllostomidae) and *Tadarida brasiliensis* (n=4; Molossidae). Regarding birds, we recorded four orders: Columbiformes, Psittaciformes, Passeriformes and Piciformes, 14 feather samples could not be identified. The prey species consumed exhibit a mass range between 13 and 160 g with an average of 46.5 g. On the other hand, the fasting blood glucose level was recorded for the bat captured at Hacienda La Venta as 99 mg/dL, while the glucose assimilation was slow, since during the one hour experiment the blood glucose levels just increased. The bat exhibited an absorption peak after 60 minutes of glucose ingestion with glucose levels of 225 mg/dL (Figure 6; Camacho *et al.* 2024).

Discussion

Morphology. The morphometric data reported in this study (Table 1) does not differ noticeable from the previous published morphometric data of *V. spectrum* (Esquivel *et al.* 2020), indicating little variability among the Colombian populations. However, as far as we know our study is the first providing external morphometric measurements for a neonate. Esquivel *et al.* (2020) pointed out that differences observed in the ear length and forearm could be explained by the way the collectors historically took this measurement in the former and, in the latter, with clinal variation also observed in other bat species (Kelly *et al.* 2018); aspects that we did not address in this study. Our specimens exhibit a standard fur coloration (reddish brown, Figure 2); however, it has been reported that specimens of *V. spectrum* could show variation in external characteristics such as fur coloration, ranging from grayish to reddish brown (Navarro and Wilson 1982). This data is important for comparing morphological measurements with information obtained in the past and captures from different altitudes or ecosystems, which must be explored to evaluate whether the differences are associated with clinal variation or environmental conditions.

Historical distribution and ecological affinity. The distribution of *V. spectrum* is generally associated with well-conserved habitats, with forest cover as a key factor

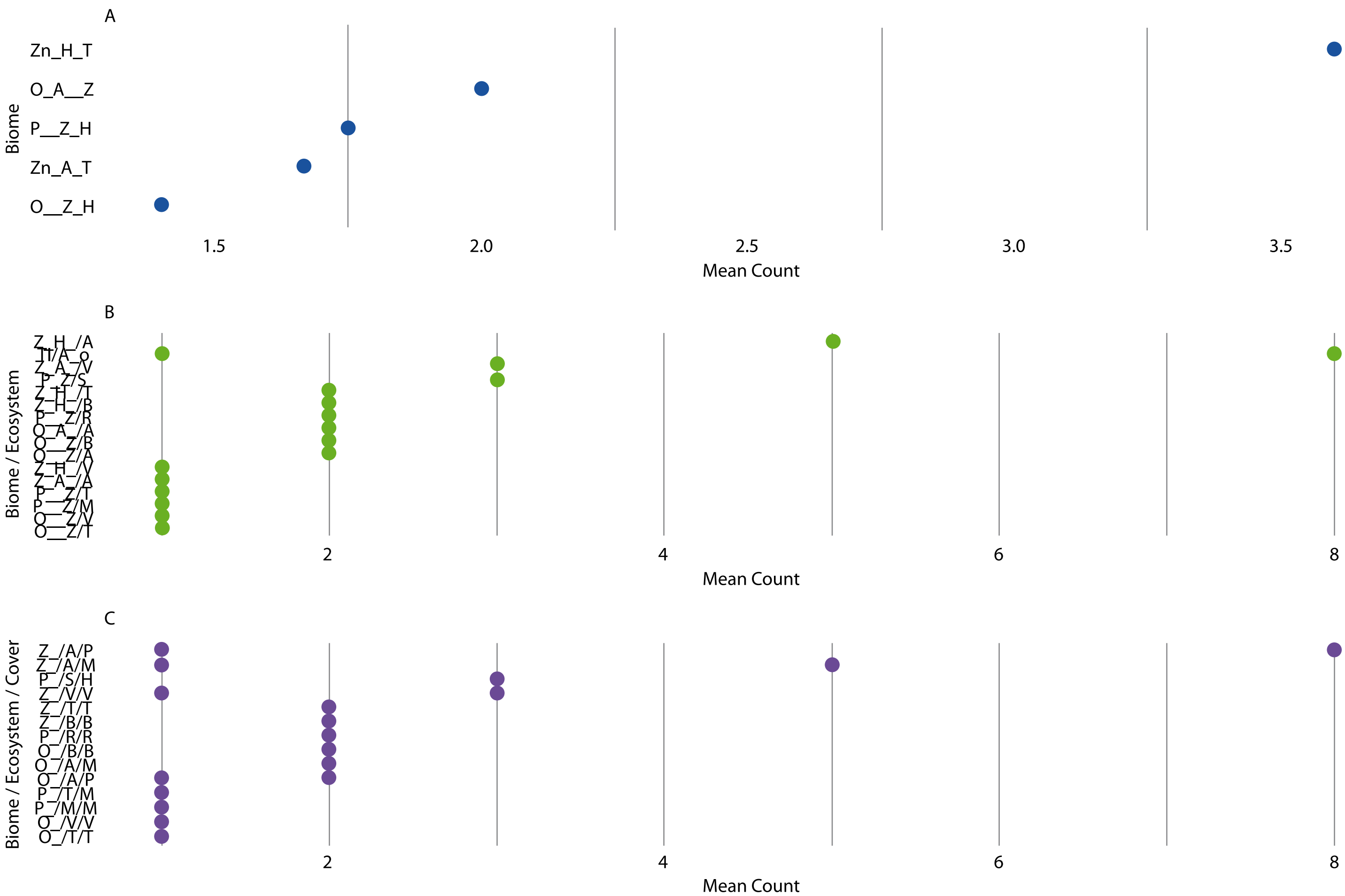

Figure 5. Mean *Vampyrum spectrum* counts across hierarchical ecological levels in Colombia. The figure displays the average number of *V. spectrum* records at three nested spatial scales: (A) Biome, (B) Ecosystem nested within Biome, and (C) Cover nested within Ecosystem and Biome. Each point represents the mean count for a given category, with labels abbreviated for clarity. The visualization highlights the structured variation in counts across ecological contexts, supporting the conclusion that habitat use by *V. spectrum* is influenced by multi-scale environmental factors rather than vegetation cover alone. For acronyms see IDEAM et al. (2017).

influencing its occurrence (Solari 2018). However, our historical and current vegetation cover analyses indicate that the species is undergoing significant environmental changes, 43% (Figure 3). The earliest recorded observation of *V. spectrum* in Colombia dates to 1942 (Rivas-Pava *et al.* 2007). Unfortunately, the oldest available data on forest and non-forest cover in the country is from 1990 (IDEAM 2019), leaving a 48-year gap in our understanding of habitat availability and preferences for the species.

Although we initially hypothesized that *V. spectrum* would exhibit a strong dependence on vegetation cover, with higher occurrence in well-conserved areas, our results did not support this assumption. Instead, the Bayesian hierarchical model revealed that its distribution is better explained by a multi-scale ecological structure encompassing Biome, Ecosystem, and Cover. Visualizations of the mean counts by Biome, Ecosystem, and Cover (Figure 5) illustrate clear differences in *V. spectrum* records across these nested spatial scales. The model's random intercepts captured meaningful variability at each level, with posterior estimates indicating non-negligible standard deviations for Biome (0.37), Ecosystem within Biome (0.30), and Cover within Ecosystem and Biome (0.29).

These findings suggest that *V. spectrum*'s habitat preferences are not solely determined by vegetation integrity, but rather by a multifactorial set of ecological drivers acting across different spatial and temporal scales. This interpretation aligns with the results of Aguiar *et al.* (2015), who demonstrated that the distribution of Tonatia saurophila is likely shaped by a complex interplay of factors including climate, topography, habitat structure, and potential evolutionary divergence. Such parallels underscore the importance of considering hierarchical environmental and a broader ecological and evolutionary contexts when modeling species distributions, particularly for wide-ranging species like *V. spectrum*. The apparent absence of a simple vegetation-cover dependency underscores the complexity of habitat selection in heterogeneous landscapes such as those found in Colombia and calls for more integrative approaches that account for spatial structure and ecological interactions.

Armenteras *et al.* (2013) estimated that between 1990 and 2005, Colombia experienced an annual deforestation rate of 0.62%, equivalent to approximately 341,071 hectares (ha) of forest lost per year. The habitat alterations observed in the forest and non-forest cover map for the period 1990–2017 (Figure 3), underscore the extensive habitat loss that has occurred over time. This pattern suggests that Spectral bat's environments are likely to continue undergoing transformation. Habitat loss and shift in land use in Colombia has been primarily driven by agricultural expansion and livestock farming, which are closely linked to deforestation (González *et al.* 2011; Negret *et al.* 2019). Notably, the Andean region, where a significant proportion of *V. spectrum*'s records are concentrated, has experienced some of the highest deforestation rates in the country (Etter *et al.* 2006).

National-scale updates on forest cover changes since 2017 are still pending. However, recent reports indicate that the deforestation rates have declined in recent years after peaking in 2017, when 425,000 ha of forest were lost. Notably, in 2023 primary forest loss decreased 49% compared to 2022, when 266,000 ha were deforested, according to Global Forest Watch (World Resources Institute 2024). The status of the Tropical Dry Forest (TDF) remains critical, ranking among the most threatened ecosystems globally. In Colombia, over 92% of its original vegetation cover has been lost *(*Pizano and García 2014). This decline is primarily driven by human activities, such as livestock grazing, agricultural expansion, mining, and timber harvesting (Álvarez-Álvarez *et al.* 2018; Scolozzi *et al.* 2012; Ruiz *et al.* 2013). In Valle del Cauca, most of the remaining TDF fragments are scarce and are currently under protection due to their valuable vegetation cover and unique plant formations (Alvarado-Solano and Otero-Ospina 2015; Salazar *et al.* 2002). However, knowledge about smaller TDF fragments and their associated species remains limited.

This study documents the second record of the species in the Valle del Cauca, and the first within the department's TDF. Statistical analysis revealed that the distribution of *V. spectrum* is better explained by a multi-scale ecological structure encompassing Biome, Ecosystem, and Cover (Figure 5), suggesting that the species' habitat preferences are not solely driven by vegetation integrity, but rather by a combination of ecological factors operating at different spatial scales. In Colombia, information is scarce about the species' association with specific biomes, or vegetation cover types occupied by *V. spectrum*. Esquivel *et al.* (2020) identified that *V. spectrum* mainly inhabits primary and secondary forests (Cabrera 2011; Esquivel and Rodríguez-Bolaños 2018), tropical dry forests (Maria 2004), and sub-Andean forests, particularly in areas with high precipitation. The presence of *V. spectrum* primarily across diverse habitats with varying degrees of human disturbance suggests a potential tolerance to habitat transformation. This finding aligns with our results, which show an association between the species and the tropical humid zonobiome and higher occurrences in grasslands and agricultural mosaics (Figure 3). One possibility is the species' adaptability to habitat changes. Given its extensive home range (Vehrencamp *et al.* 1977; Solari 2018), *V. spectrum* likely moves between roosting sites to water and food resources, navigating through fragmented, degraded areas. Additionally, grasslands may provide abundant and easily accessible prey in simplified environments with fewer obstacles and reduced prey refuges.

Roost availability is a critical factor for the persistence of *V. spectrum*, as the species relies on large, mature trees with natural cavities and caves (Altringham 2011). Our results suggest that the species has been recorded in highly transformed landscapes, raising questions about the quality of available roosting sites. An analysis of the forest structure in 10 tropical dry forest fragments in central-northern Valle del Cauca, including La Venta (the site where our specimen of *V. spectrum* was captured) reveals that most trees belong to the smallest diameter classes, with fewer individuals in intermediate and larger size categories (Saldaña and Moncaleano 2021). However, La Venta exhibits a more balanced diameter class distribution, indicating a higher presence of large trees compared to other remnants assessed (Saldaña and Moncaleano 2021).

These findings suggest that although *V. spectrum* can occupy fragmented landscapes, the scarcity of large-diameter trees in many tropical dry forest remnants may limit its long-term persistence. Previous studies have found that large-bodied bat species strongly depend on trees with natural cavities or artificial structures when natural roost availability is low (Dinets 2016). Given the advanced transformation of Colombia's tropical dry forest, the conservation of large trees and the restoration of forest fragments with potential for cavity development could be key strategies for protecting the species.

Diet and sugar assimilation. There are some reports on the diet of Spectral bat across its distribution, most of them conducted in Central America. However, it is difficult to determine the identity of the consumed species from stomach contents due to gastric destruction of the samples (Casebeer 1963; Petterson and Kirmse 1969). Therefore, finding a roost like the one reported here is important to document the identity of the Spectral bat's preys. This is the first diet report for the species in Colombia and in a sub-xerophytic forest ecosystem (Esquivel *et al.* 2020). The area where the diet information comes from is characterized by shrub and sub-arboreal deciduous or semi-deciduous strata typical of the families Fabaceae, Euphorbiaceae, Cactaceae, Bignoniaceae, and Rutaceae of dry forest. The sub-xerophytic forest of the Patía Valley has a high degree of anthropogenic intervention and differs in structure from other dry forests in Colombia, having some of the smallest patches in the country (Cabrera-Ojeda *et al.* 2016), which poses significant threats to the Spectral bat in this ecosystem.

Through the analysis of remains in refuges, up to 18 bird species have been recorded (Vehrencamp *et al.* 1977), while Martínez-Fonseca *et al.* (2022) presented a list of 27 species detected through barcoding from feces, of which *Leptotila verreauxi* and *Phyllostomus discolor* are shared with this study. Some new contributions to the diet of

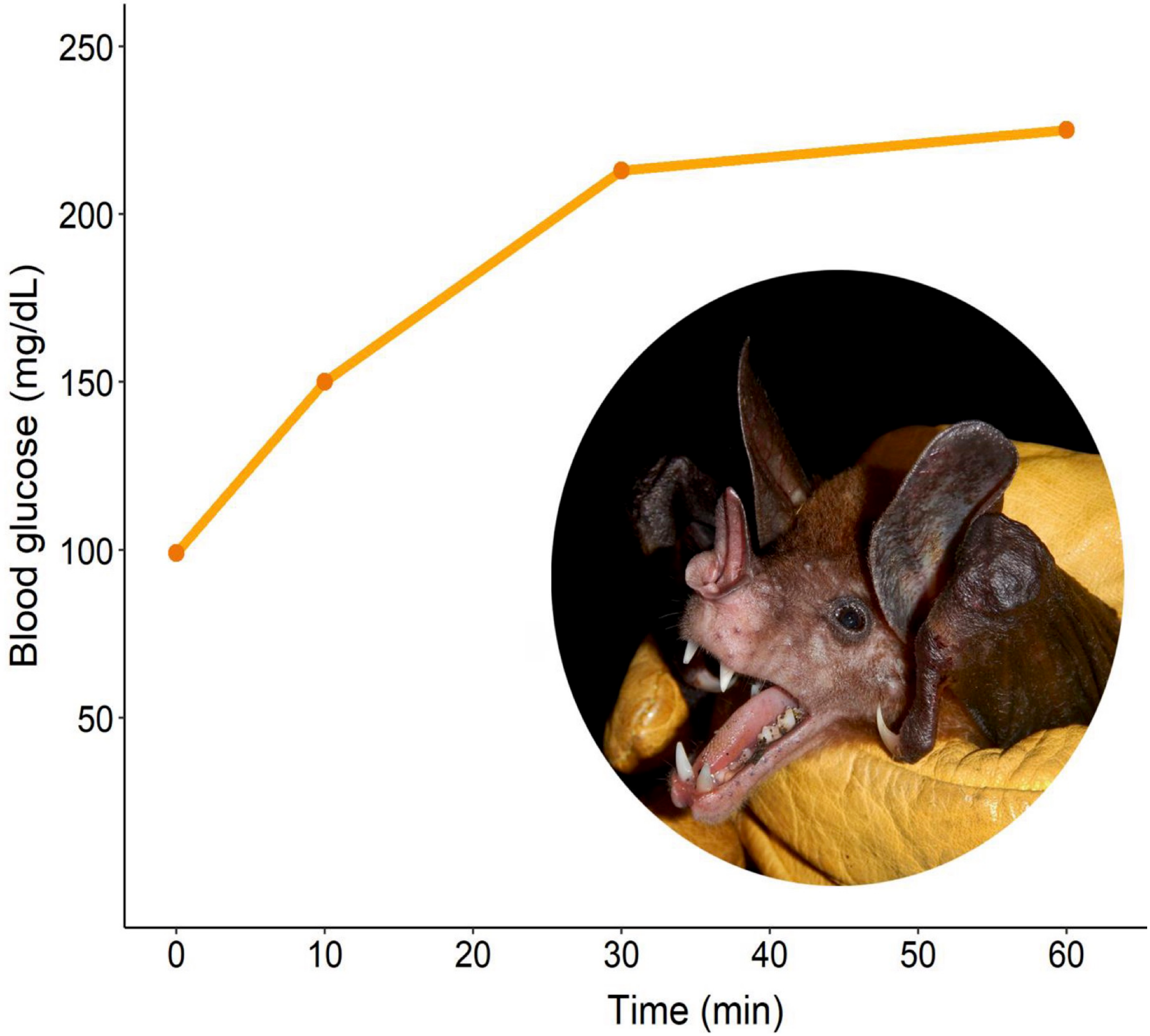

Figure 6. Sugar assimilation curve for the individual of *Vampyrum spectrum* captured in Hacienda La Venta, Bugalagrande, Valle del Cauca, Colombia. Adapted from Camacho et al. (2024).

the *V. spectrum* are the birds *Zenaida auriculata*, *Pheuticus aureoventris*, *Pyrocephalus rubinus*, *Colaptes puntigula*, *Forpus conspicillatus*, and *Thamnophilus multristriatus*. These species range in weight from 14 to 125 g, like those reported in other studies (Vehrencamp *et al.* 1977; Martínez-Fonseca *et al.* 2022). The reported diet does not seem to show a specific preference for any prey; however, the presence of non-passerine birds stands out. It has been suggested that the olfactory sense of the Spectral bat may play an important role in hunting these types of birds, which can have a strong odor and occupy gregarious perches (Vehrencamp *et al.* 1977). The new mammal records in this diet are the cricetid rodents *Zygodontomys brunneus*, *Reithrodontomys mexicanus*, and the molossid bat *Tadarida brasiliensis*. *R. mexicanus* and *T. brasiliensis* are the first confirmed records for TDF in the Nariño department, which highlight the importance of predator refugees' analysis for the documentation of poorly known species. It has been reported that the foraging of Spectral bats is limited to the mid and upper strata of the forest, catching birds and mammals that rest at a certain height, limiting their ability to forage at lower heights (Vehrencamp *et al.* 1977). However, it seems that some foraging strategies include low flights (Pacheco-Figueroa *et al.* 2022). The rodents recorded in *V. spectrum*'s diet in this study are typically on the ground, especially *Z. brunneus*, an open grassland and shrub mouse (Voss 1991), suggesting that the Spectral bat actively hunts over lower forest strata. Likely, olfaction is also an important factor in the search for mammals, as the recorded species, like bats, are also characterized by strong body odors (Nielsen *et al.* 2006; Kwiecinski 2006).

In terms of the Spectral bat physiology, we observed what was expected for an organism with a low-sugar diet, a slow glucose assimilation (Figure 6, Camacho *et al.* 2024). During the one-hour period of the experiment the process of glucose incorporation into the tissues was never higher than the previous intestinal glucose absorption process. This demonstrates a low sugar assimilation capability compared to bats with rich-sugar diets, in which blood glucose levels decrease after 10 and 30 minutes of glucose ingestion and reach much higher blood glucose levels (Kelm *et al.* 2011: Peng *et al.* 2017; Camacho *et al.* 2024). The glucose tolerance was like the one observed in insectivorous bats (Peng *et al.* 2019), which is very likely due to its carnivory preferences. The species' nutrition is mostly based on proteins and very few glucoses, mainly coming from the prey's blood (birds and small mammals), so glucose absorption does not compare to the speed at which nectarivore or frugivore bat species absorb glucose (Camacho *et al.* 2024).

Conservation strategies and landscape management for V. spectrum. The conservation of the Spectral bat requires an integrated approach focused on enhancing habitat connectivity, promoting sustainable land-use practices, and involving local communities. Key strategies include creating ecological corridors (Hilty *et al.* 2021), restoring roosting trees like *Ficus* spp., *Anacardium excelsum*, and *Brosimum alicastrum* (Ramos-Perez and Silverstone-Sopkin 2018), adopting agroforestry systems (Arroyo-Rodríguez *et al.* 2019), and incentivizing landowners through ecosystem service payments (Ardila-Vargas and Estrada 2021). Long-term monitoring and collaboration with communities and conservation groups are essential for effective, lasting protection.

This study highlights urgent deforestation and habitat loss in Colombia, emphasizing the need for focused conservation efforts on protecting and restoring critical habitats. The likely *V. spectrum*'s resilience to habitat changes suggests conservation should also include the already transformed landscapes surrounding protected forests. Human activities, particularly agriculture and livestock farming, significantly contribute to habitat degradation. Therefore, conservation strategies must promote sustainable land use and mitigate anthropogenic impacts. Our study offers valuable ecological insights that are essential for future conservation planning. It highlights the importance of maintaining ongoing monitoring of habitat changes and species distributions to effectively adapt strategies. Additionally, it is critical to raise awareness of *V. spectrum*'s ecological significance to support these initiatives. Ultimately, although more research is needed to fully understand the species' habitat needs, it is crucial to advocate for policies that protect fragmented ecosystems, enhance connectivity, promote sustainable practices, and conserve preys' diversity for the long-term survival of the species. Further studies should focus on understanding how the species deals with landscape transformation in terms of physiological stress and ecological adaptability. Integrative studies are needed to assess what the optimal and suboptimal habitat characteristics for the species are, to evaluate if the species distribution range or home range is expanding or contracting, and how large the populations remaining in extremely disturbed and fragmented ecosystems like the Tropical Dry Forest.

Acknowledgments

We thank the Sistema General de Regalias for funding this project. We thank the Corporacion Autonoma Regional del Valle for issuing the collect permit 100 No. 1122 of October 23, 2018, for the project "Contribución a la conservación del Bosque Seco Tropical del Valle del Cauca a través del fortalecimiento Valle del Cauca occidente". Additionally, we would like to acknowledge the contributions of our fellow team members for their collaboration and eagerness to learn throughout the project. We want to thank F. Ramirez for the help provided to identify the diet content published in this study. We are thankful to the curators of the zoological collections housing the specimens referenced in this study. Our gratitude also goes to the Laboratory of Images at Universidad del Valle for their assistance with the cranial imaging. Lastly, we appreciate the anonymous reviewers for their valuable and constructive feedback on the previous version of this paper.

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Associated editor: Sergio Solari
Submitted: April 8, 2025 Reviewed: July 3, 2025
Accepted: July 8, 2025 Published on line: August 4, 2025