

Article

Addressing the Wallacean Shortfall in Neotropical Mammals: Documented Distribution and Late-Quaternary Climatic Suitability of a Poorly Known Forest Bat

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Abstract

Distributional gaps in poorly documented Neotropical mammals often reflect the combined effects of ecological filtering, low detectability, taxonomic uncertainty, and incomplete sampling. We reassessed the documented distribution of *L. brachyotis* (Dobson, 1879), a rarely collected forest-dwelling phyllostomid bat, using an expanded occurrence dataset and specimen-based validation. Independently, we used ecological niche models to characterize climatic suitability under current and paleoclimatic conditions. We compiled 125 documentary or specimen records from published sources and museum material, including new voucher-based records from southern Ecuador and northern Colombia, and consolidated them into 121 reviewed unique locality-coordinate units. After environmental screening and cell-level deduplication, 115 unique presence cells were used for model calibration. The best-supported model used linear, quadratic, and hinge features with a regularization multiplier of 2.5 and performed significantly better than null-model expectations. Under current conditions, climatic suitability was broad but spatially heterogeneous across northern South America, with additional suitable areas in Mesoamerica, the Andean–Amazonian interface, central Brazil, and southeastern Brazil. Temporal projections identified recurrent areas of climatic suitability across northern South America, but were interpreted as climatic context rather than direct evidence of historical occupancy or demographic continuity. The new records indicate that the documented distribution remains incomplete along its margins. Our results support a revised interpretation of *L. brachyotis* as a rarely recorded humid-forest bat with a coherent Amazonian–Guianan core and peripheral extensions consistent with the combined influence of climatic suitability, habitat heterogeneity, and incomplete sampling.



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1. Introduction

Biodiversity patterns emerge from the interplay of two overlapping geographies: one rooted in ecological and evolutionary processes that shape species distributions and community structure, and another based on the geography of knowledge, which is determined by where organisms have been collected, how taxonomists have focused on different

taxa, the methods used for species identification, and the variable digital accessibility of records [1]. Those patterns reflect both the ecological and evolutionary processes that shape species distributions and the uneven geography through which those distributions are documented. Human knowledge of species occurrence is built from observations and specimens, but these records are spatially incomplete and strongly influenced by accessibility and sampling effort [2]. Consequently, poorly sampled regions may appear artificially species-poor, whereas intensively surveyed areas may seem disproportionately diverse. This mismatch between the actual distribution of species and their geographic documentation constitutes the Wallacean shortfall [3,4]. It remains one of the main obstacles to interpreting biodiversity patterns and conservation priorities in poorly sampled regions [5–7]. In rare species, this shortfall can create apparent range gaps that may reflect missing data rather than true absences.

The Wallacean shortfall rarely acts alone. Taxonomic uncertainty can compromise the reliability of occurrence records, while limited ecological knowledge can obscure the environmental conditions associated with species presence [3]. These limitations are especially consequential for rare Neotropical mammals, for which additional records are most informative when they come from spatially or environmentally underrepresented areas [7,8]. Natural history collections are therefore essential for reducing distributional uncertainty because they provide verifiable specimens and associated data, although their use in South America remains constrained by uneven digitization, infrastructure limitations, and restricted access to type material [9]. Amazonia contains exceptional biodiversity, but species distributions remain unevenly documented because collection effort is concentrated near rivers, roads, protected areas, and historically active institutions [10]. This spatial bias complicates the distinction between genuine biogeographic structure and sampling artifacts. Verified peripheral records may therefore reveal discrepancies between observed occurrences and established range polygons [6].

This distinction is especially relevant to the biogeographic relationship between Amazonia and the Atlantic Forest, two major forest domains currently separated by the South American dry diagonal, whose Brazilian portion is represented mainly by the Cerrado and Caatinga [11,12]. This region has often been interpreted as a barrier for forest-associated taxa [12]. However, historical connections between Amazonia and the Atlantic Forest were probably spatially complex. Ecological niche models have identified multiple potential climatic connections during the Last Glacial Maximum, rather than a single uniform corridor [13]. Palaeoecological data also indicate that South American seasonally dry forests had regionally heterogeneous Late Quaternary histories [14]. The dry diagonal should therefore not be reduced to a simple barrier. It contains a heterogeneous mosaic of open formations, dry forests, wetlands, and humid enclaves. These internal contrasts can affect the movement and persistence of forest-associated species.

Forest bats may be especially affected by incomplete documentation because ground-level mist nets underrepresent species using higher strata, forest interiors, or specialized flyways [15,16]. Low detectability can therefore intensify the Wallacean shortfall in this group [8,17]. *Lamproncycteris brachyotis* (Dobson, 1879) is a strong example of this problem. The species is widely distributed in the Neotropics, but it is rarely captured and remains poorly represented in many regional inventories [18–20]. It is generally associated with humid forests, although records from secondary forests, clearings, and mesic environments within broader open landscapes have also been reported [21]. Its foraging ecology and habitat use suggest a dependence on forest structure that may influence detectability and local occurrence [22]. This combination of broad range, low detectability, and apparent discontinuity makes *L. brachyotis* an ideal case for reassessing the boundary between true biogeographic structure and incomplete documentation.

Rocha et al. [23] placed *L. brachyotis* within the Amazonian–Atlantic Forest disjunction problem by testing whether apparent absences across the dry diagonal reflected true fragmentation or incomplete sampling. Their models supported a strong association with forested environments and identified suitable conditions in humid enclaves of northeastern Brazil. These results left unresolved whether the species’ apparent fragmentation reflects historical disjunction, heterogeneous ecological filtering, or a Wallacean shortfall, amplified by low detectability and uneven sampling.

Here, we reassess the documented distribution of *L. brachyotis* using an expanded, reviewed occurrence dataset, including newly documented voucher specimens. We ask how this expanded evidence changes our understanding of the species’ documented geographic pattern and whether the apparent fragmentation of records reflects a strongly disjunct pattern or a coherent humid-forest core with peripheral gaps. Independently, we use ecological niche models to characterize current climatic suitability and to examine how suitable climatic conditions may have varied through the late Quaternary. We then ask how these present and past climatic suitability patterns inform the biogeographic context of the remaining distributional gaps, particularly in relation to the South American dry diagonal, historical Amazonian–Atlantic Forest connections, and the Wallacean shortfall, without treating modeled suitability as evidence of realized occupancy.

2. Materials and Methods

2.1. Occurrence Data Acquisition and Validation

Occurrence data for *L. brachyotis* were compiled from published literature, direct examination of museum specimens, and photographic documentation of type material. Bibliographic records were obtained by reviewing studies reporting occurrences across the known range of the species. Voucher specimens were examined in the Museo de la Estación Biológica de Rancho Grande (EBRG), Venezuela; the Museo de Zoología de la Universidad Técnica Particular de Loja (MUTPL), Ecuador; the Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador; and the Mammal Collection “Alberto Cadena García” of the Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia. Original photographs of the holotype of *Schizostoma brachyote* Dobson, 1879 (MNHN-ZM-MO-1876-1074, Muséum national d’Histoire naturelle, Paris, France) and the holotype of *Micronycteris* (*Lampronnycteris*) *platyceps* Sanborn, 1949 (FMNH 61942, Field Museum of Natural History, Chicago, IL, USA) were also evaluated for comparative purposes. The procedures used for morphological validation are described in Section 2.3.

We reviewed all records for taxonomic and geographic consistency and checked geographic coordinates against the associated locality information. When needed, we georeferenced or corrected coordinates using specimen labels, published locality descriptions, gazetteers, and Google Earth Pro version 7.3.4.8248. The occurrence-level dataset retained one row per documentary or specimen record. We consolidated independent records sharing the same locality-coordinate combination into a single unique locality-coordinate unit for distributional mapping and ecological niche modeling.

The final database comprised 125 documentary or specimen records consolidated into 121 reviewed unique locality-coordinate units. Appendix A provides a formatted gazetteer of the 121 locality units. Supplementary Dataset S1 provides complete occurrence- and locality-level data, including coordinates, voucher information when documented, source categories, taxonomic validation evidence, and ecological niche modeling status.

2.2. Ecological Niche Modeling

We estimated climatically suitable areas for *L. brachyotis* under current and past climatic conditions using an ecological niche modeling framework implemented through

Wallace 2.0 [24]. The analysis incorporated validated occurrence data, bioclimatic predictors, an operationally defined accessible area, spatially structured model evaluation, and parameter tuning intended to balance model fit and complexity.

2.2.1. Occurrence Data and Environmental Predictors

Occurrence data were derived from the 121 unique locality-coordinate units described above. During environmental data extraction, we excluded five locality units because one or more bioclimatic variables had missing values at their coordinates, leaving 116 environmentally valid localities. To avoid pseudoreplication at the environmental data's spatial resolution, we reduced occurrence records within the same 2.5 arc-minute environmental grid cell to a single presence. Two records fell within the same environmental cell; therefore, we used 115 unique presence cells for model calibration.

We initially considered 19 continuous bioclimatic variables from WorldClim 2 [25], representing the 1970–2000 period at a spatial resolution of 2.5 arc-minutes, to characterize climatic conditions. To reduce redundancy among environmental predictors, we calculated pairwise Pearson correlations across the calibration area. Predictor pairs with $|r| \geq 0.70$ were considered highly correlated. Thirty-four pairs met this criterion. Within groups of correlated predictors, we retained variables representing distinct, ecologically interpretable dimensions of temperature and precipitation. The final predictor set comprised annual mean temperature (BIO1), mean diurnal range (BIO2), temperature seasonality (BIO4), precipitation of the wettest month (BIO13), precipitation of the driest month (BIO14), precipitation seasonality (BIO15), precipitation of the warmest quarter (BIO18), and precipitation of the coldest quarter (BIO19). No pair among the retained predictors exceeded $|r| = 0.70$; the highest absolute correlation was $|r| = 0.671$ between BIO13 and BIO19. Pairwise correlations among the retained predictors are shown in Supplementary Figure S1.

2.2.2. Calibration Region and Background Sampling

We defined the accessible area used for model calibration as a single continuous region encompassing the known occurrence localities. We constructed a minimum convex polygon around the marginal localities and added a 0.5° buffer to account for geographic uncertainty and potential accessibility in poorly sampled areas. We masked environmental layers to this region using the raster R package (version 2.4-20) and the mask function, and sampled background environmental data only within the resulting calibration area.

We sampled 10,000 background points within the resulting calibration area. We restricted background sampling to this operationally defined accessible area for all candidate models and model evaluations.

2.2.3. Model Tuning, Selection, and Final Fitting

We estimated climatic suitability using the maximum entropy algorithm implemented in Maxent version 3.4.4 through Wallace 2.0 [24] and evaluated candidate model settings using ENMeval version 0.2.0. We explored model complexity using three feature-class combinations: linear and quadratic (LQ); linear, quadratic, and hinge (LQH); and linear, quadratic, hinge, and product (LQHP). We evaluated each combination with regularization multipliers from 0.5 to 5.0 in 0.5 increments, yielding 30 candidate parameterizations.

We evaluated models using the hierarchical checkerboard2 partitioning method, which assigned occurrence and background data to four geographically structured evaluation bins. The 115 unique presence cells were distributed among these bins as 25, 27, 36, and 27 occurrences. For each candidate parameterization, we trained and evaluated models across the four spatial folds, and summarized validation statistics as mean $\pm$ SD. We used

this spatially structured cross-validation instead of random train–test partitions to reduce spatial dependence between training and validation data.

Candidate parameterizations were compared using the Akaike Information Criterion corrected for small sample size (AICc), validation area under the receiver operating characteristic curve (AUC), the difference between training and validation AUC (AUCdiff), the Continuous Boyce Index (CBI), and the 10% training omission rate (OR10). Model selection prioritized the lowest AICc while considering predictive performance and omission rates. The best-supported parameterization used linear, quadratic, and hinge features (LQH) with a regularization multiplier of 2.5. After selecting model complexity, we fitted the final model using all 115 unique presence cells and 10,000 background points sampled within the calibration area. We retained continuous suitability predictions for spatial interpretation rather than converting model outputs into binary suitable–unsuitable maps.

To assess whether model performance exceeded chance expectations, we conducted a null-model evaluation following the general framework of Raes and ter Steege [26] using the null-model implementation in ENMeval. We generated 100 null models using the same parameterization selected for the empirical model (LQH features, RM = 2.5) and evaluated them using the same hierarchical four-fold checkerboard partitioning scheme. We compared validation metrics from the empirical model with the corresponding null distributions using standardized effect sizes (z-scores) and associated *p*-values.

2.2.4. Paleoclimatic Projections and Extrapolation Assessment

We projected the final model under current conditions and three paleoclimatic scenarios: the mid-Holocene, approximately 6000 years BP; the Last Glacial Maximum, approximately 22,000 years BP; and the Last Interglacial, approximately 125,000 years BP. The mid-Holocene and Last Interglacial layers were available at 30-arc-second resolution, whereas the Last Glacial Maximum layers were available at 2.5-arc-minute resolution [27].

We evaluated environmental extrapolation using clamping and multivariate environmental similarity surfaces generated by Maxent. We used these diagnostics to identify regions with climatic conditions outside the environmental range represented in the calibration data. We therefore interpreted paleoclimatic projections as broad patterns of climatic suitability rather than direct estimates of realized occupancy, demographic continuity, or precise historical range boundaries.

2.3. Morphological Validation

Morphological validation focused on voucher specimens from newly documented and selected previously reported localities, particularly records that extend or refine the known distribution of *L. brachyotis*. Species identification was assessed using external and cranial characters traditionally employed to distinguish *L. brachyotis* from related micronycterine bats (e.g., [18,28,29]). External characters included pelage coloration, ear morphology, noseleaf structure, lower-lip morphology, and wing proportions. Cranial assessment considered skull shape, rostral inflation, basisphenoid pits, zygomatic breadth, and dentition.

Particular attention was given to MUTPL M-18 from Ecuador and ICN 17238 from Colombia. We compared these specimens with reference material in the consulted collections, published morphometric data, and original photographs of the holotypes of *S. brachyote* and *M. platyceps*. We evaluated the type specimens exclusively from photographic documentation and did not examine them directly. This comparative framework provided the taxonomic basis for retaining the corresponding occurrence records in the distributional and ecological niche analyses.

3. Results

3.1. Distributional Dataset and Spatial Patterns of *L. brachyotis*

A total of 125 documentary or specimen records were compiled and consolidated into 121 unique locality-coordinate units across the Neotropics (Appendix A). At the locality level, 107 units were supported exclusively by published sources, 11 were documented exclusively in the present study, and three were supported by both. The compiled dataset spans from southern Mexico through Central America to northern and central South America (Figure 1). In Mesoamerica, documented localities are distributed discontinuously from southern Mexico to Panama, with most concentrated along the Caribbean slope. In South America, documented localities are unevenly distributed and strongly concentrated in northern and Amazonian regions. The 121 unique locality-coordinate units were distributed across 16 countries and territories. Brazil contained the largest number of documented localities ($n = 31$), followed by Colombia ($n = 22$), Venezuela ($n = 14$), Mexico ($n = 12$), and Trinidad and Tobago ($n = 11$). Panama and Peru each contributed six localities, Costa Rica four, and Belize and Nicaragua three each. Bolivia, Ecuador, and Guatemala each contributed two localities, whereas French Guiana, Guyana, and Surinam each contributed one locality. Across southern Central America and northern South America, documented localities form a broadly continuous geographic belt from eastern Panama through Colombia and Venezuela to the Guiana Shield.

South of the Amazon basin, documented localities are sparse and geographically isolated. These include localities in southern Amazonia and southeastern Brazil, with no evidence of continuous occurrence across intervening regions (Figure 1). In contrast, the Amazon and Guianan regions show a dense aggregation of documented localities, defining the core of the species' documented distribution.

3.2. Model Calibration and Performance

Model tuning across the 30 candidate parameterizations identified a model with linear, quadratic, and hinge features (LQH) and a regularization multiplier of 2.5 as the best-supported configuration. This model contained 10 non-zero coefficients and had the lowest AICc among the evaluated parameterizations ($AICc = 2997.745$; $\Delta AICc = 0$). Spatially structured four-fold cross-validation yielded a mean validation AUC of 0.685 ± 0.041 , an AUC difference (AUCdiff) of 0.044 ± 0.034 , a mean Continuous Boyce Index (CBI) of 0.750 ± 0.085 , and a 10% training omission rate (OR10) of 0.130 ± 0.076 .

The selected empirical model performed significantly better than expected under the null-model distribution. Mean validation AUC was 0.685 ± 0.041 for the empirical model compared with 0.508 ± 0.025 for the 100 null models ($z = 7.002$, $p < 0.001$), whereas mean validation CBI was 0.750 ± 0.085 compared with -0.004 ± 0.137 for the null models ($z = 5.490$, $p < 0.001$). The empirical model also showed a significantly lower AUCdiff than the null models (0.044 ± 0.034 vs. 0.103 ± 0.023 ; $z = -2.604$, $p = 0.0046$) and a lower OR10 (0.130 ± 0.076 vs. 0.190 ± 0.034 ; $z = -1.766$, $p = 0.0387$). These results indicate that the selected model performed better than expected from models fitted to random occurrence data under the same spatial evaluation framework.

3.3. Climatic Suitability Under Current Conditions

Under current climatic conditions (Figure 2), the model predicted broad but spatially heterogeneous climatic suitability across the documented range of *L. brachyotis*. Higher suitability was concentrated across northern South America, including portions of Colombia, Venezuela, the Guiana Shield, and northern Amazonia, broadly coinciding with the main concentration of occurrence records. Suitable conditions also extended through parts of Mesoamerica and along the Andean–Amazonian interface. Within Amazonia, pre-

dicted suitability was heterogeneous, with areas of moderate to high suitability interspersed with lower-suitability sectors. Central Brazil contained extensive areas of comparatively lower suitability, whereas locally elevated suitability persisted in parts of southeastern Brazil, including sectors associated with the Atlantic Forest. Overall, the current projection recovered a broad northern South American suitability core accompanied by spatially heterogeneous peripheral areas in Mesoamerica, the Andean–Amazonian interface, central Brazil, and southeastern Brazil.

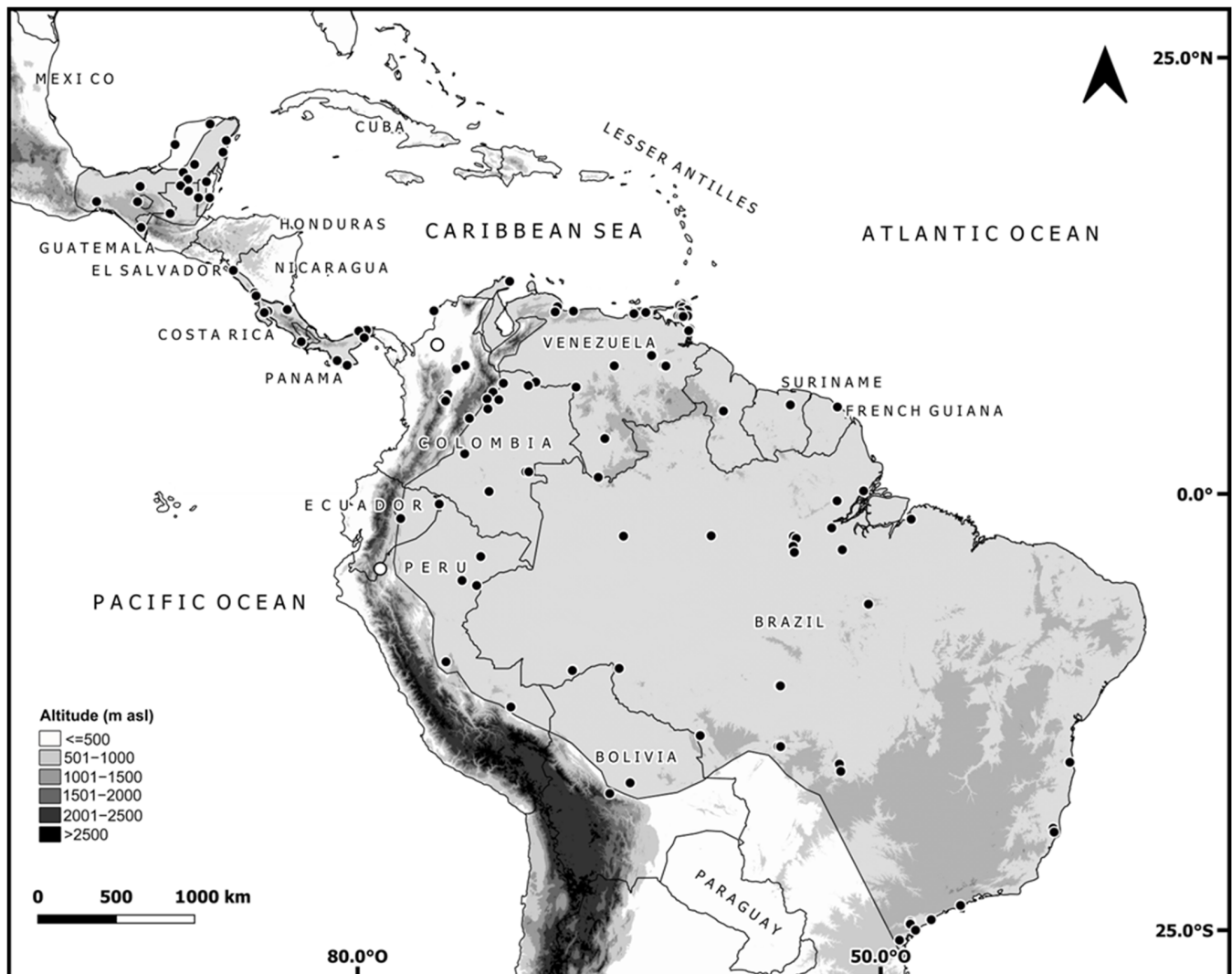


Figure 1. Known distribution of *Lamproncyteris brachyotis* in the Neotropics based on 121 unique locality-coordinate units. Filled black circles represent previously published localities or localities also supported by published evidence. Open circles identify the two new voucher-based records reported here, from Pueblo Nuevo, Córdoba, Colombia, and Maycu, Zamora Chinchipe, Ecuador. Five mapped localities were excluded from ecological niche modeling due to missing environmental data. The shaded area represents the IUCN range polygon for *L. brachyotis* provided in Solari [30].

3.4. Temporal Projections

Paleoclimatic projections (Figure 3) showed substantial temporal variation in the spatial configuration of climatic suitability for *L. brachyotis*. Nevertheless, suitable climatic conditions were repeatedly recovered across Central America and northern South America, particularly in Colombia, Venezuela, the Guiana Shield, and northern Amazonia.

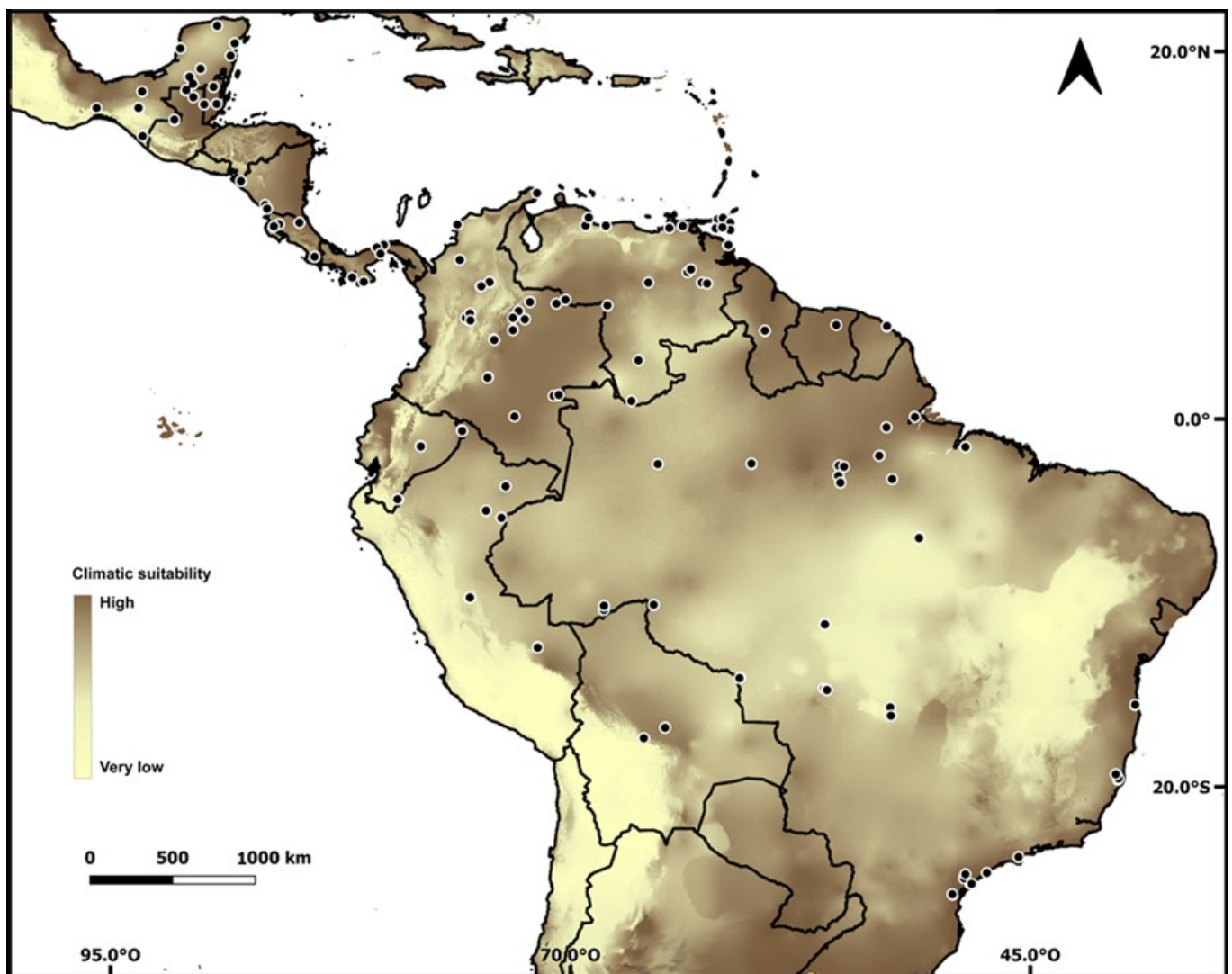


Figure 2. Current climatic suitability for *Lampronycteris brachyotis* inferred from ecological niche modeling. Darker tones indicate higher climatic suitability, and dots represent georeferenced occurrence records used to characterize the species' distribution.

The mid-Holocene projection showed extensive climatic suitability across northern South America and much of Amazonia, while suitability remained more heterogeneous toward central and southeastern portions of the continent. During the Last Glacial Maximum, suitable conditions extended broadly across Amazonia and parts of the continental interior, although their spatial configuration differed from both current and mid-Holocene conditions. The Last Interglacial projection showed a stronger concentration of suitable conditions in Central America and northern South America, with reduced suitability across substantial portions of central and southern Amazonia and central Brazil. Overall, the temporal projections identified recurrent northern South American areas of climatic suitability, while also revealing marked changes in their extent and spatial configuration among climatic periods. Extrapolation diagnostics were examined for the paleoclimatic transfers and were considered when interpreting the projections at broad spatial scales rather than as precise reconstructions of historical range limits.

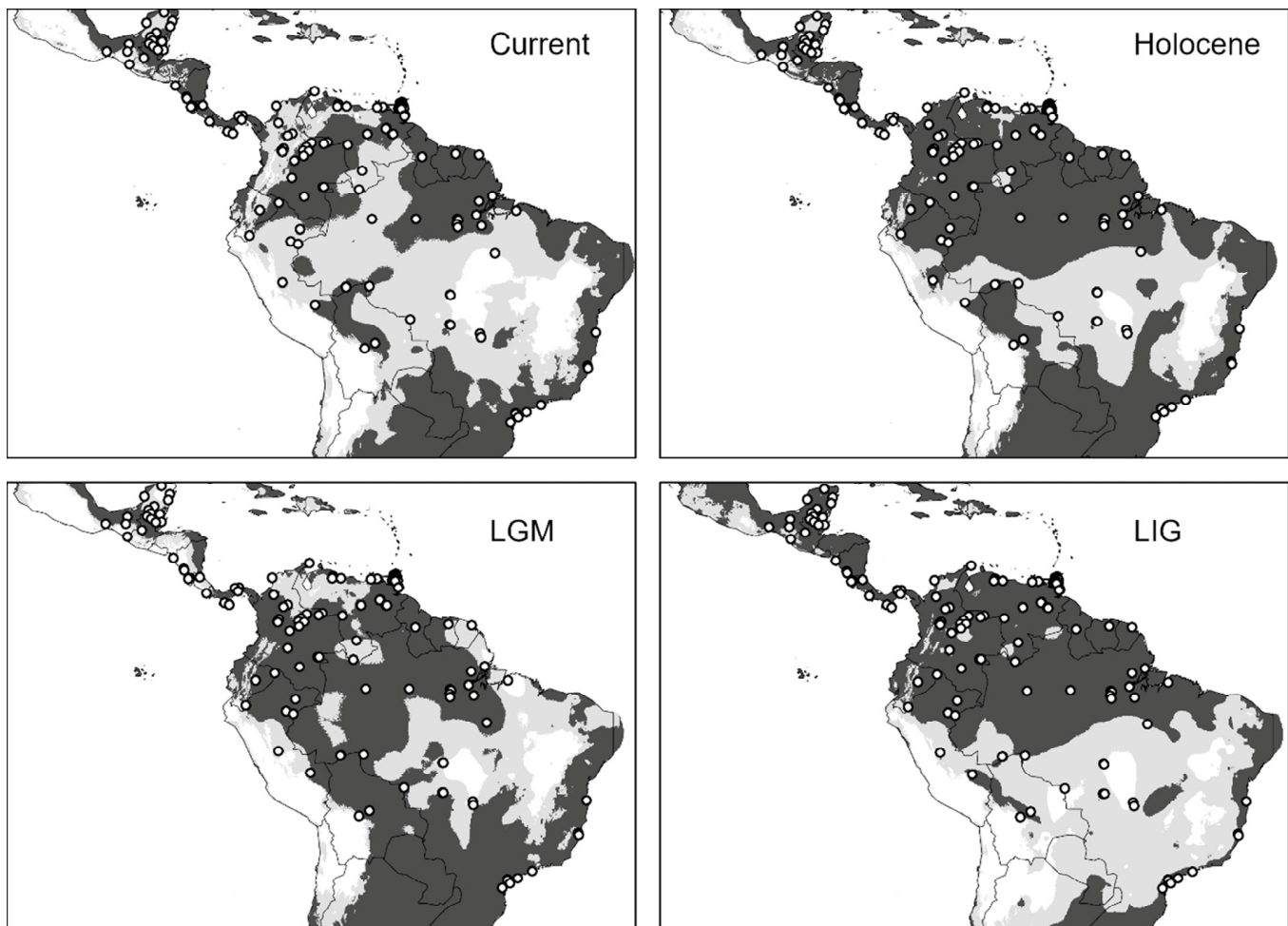


Figure 3. Ecological niche model projections for *Lampronycteris brachyotis* under current, mid-Holocene, Last Glacial Maximum (LGM), and Last Interglacial (LIG) climatic conditions. Shading represents predicted climatic suitability within each scenario, and circles represent the georeferenced occurrence records used in the distributional reassessment.

3.5. New Occurrence Records and Range Extensions

Two voucher-based records documented in this study fall outside the IUCN range polygon for *L. brachyotis* provided in Solari [30]: one from southern Ecuador and one from northern Colombia. Both records correspond to taxonomically verified specimens and represent geographically informative extensions of the known distribution of *L. brachyotis*.

In Ecuador, an adult female was collected along the Nangaritza River, at Maycu Reserve, Las Orquídeas, Zamora Chinchipe Province (-4.29388889 , -78.69694444 ; 900 m a.s.l.). The specimen (MUTPL M-18), deposited in the Museo de Zoología of the Universidad Técnica Particular de Loja, represents the second confirmed record for the country and the first documented occurrence from southern Ecuador. This locality lies along the Andean–Amazonian interface and expands the confirmed distribution of the species within the northwestern Amazonian region. The habitat and live individual are shown in Figure 4. In Colombia, specimen ICN 17238, deposited in the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, was collected in Pueblo Nuevo, Hacienda Praga, Department of Córdoba (8.55055556 , -75.42694444 ; Appendix A). This record extends the documented occurrence of the species into a poorly represented sector of northern Colombia. Figure 1 shows these records as open symbols, while previously published records appear as black symbols.

Appendix A provides complete locality data, including geographic coordinates, voucher information, and source category.

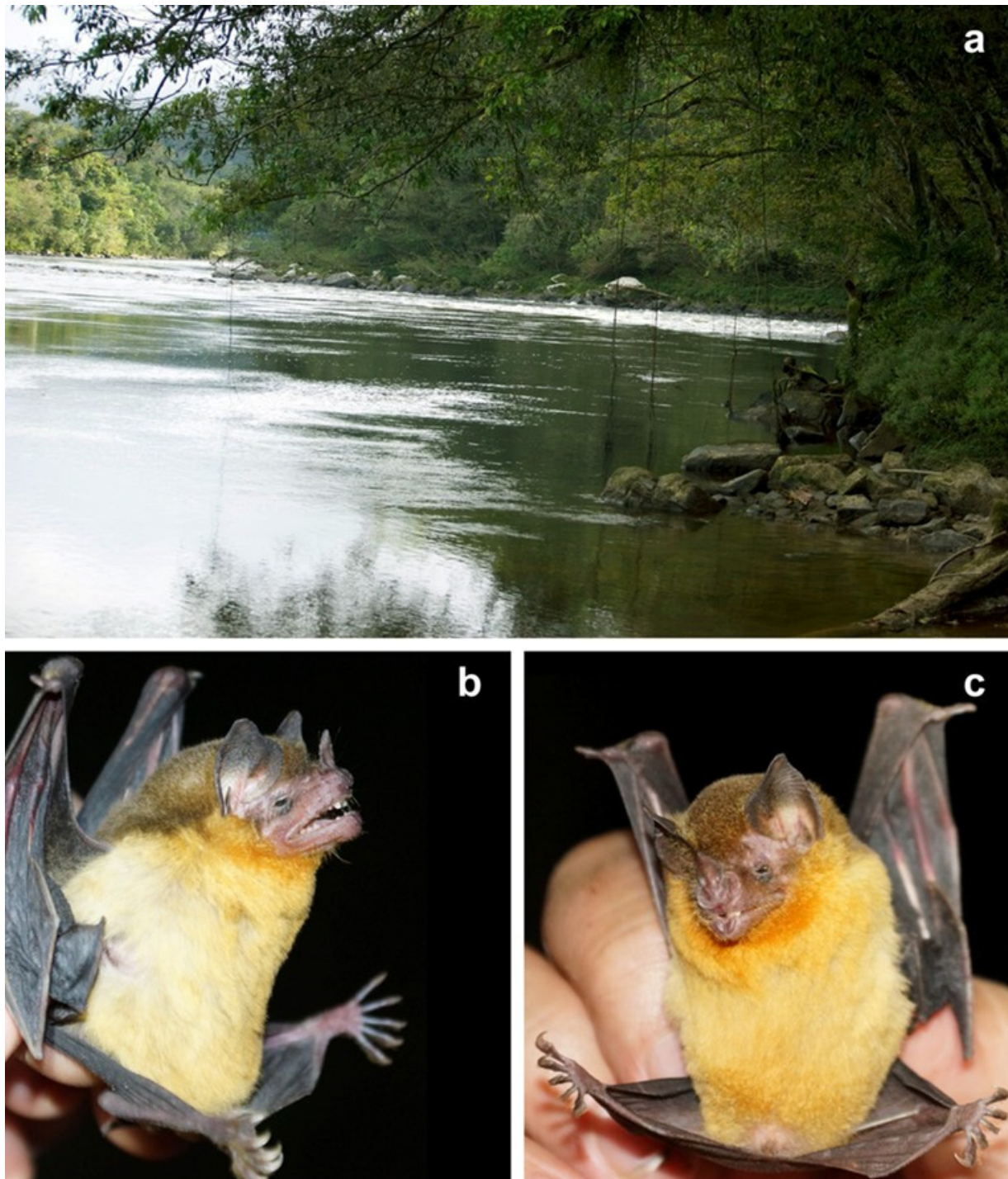


Figure 4. Habitat and live individual of *Lampronnycteris brachyotis* from Maycu Reserve, Las Orquídeas, Zamora Chinchipe, southern Ecuador. (a) Humid riparian forest along the Nangaritza River, where the specimen was collected. (b,c) Live adult female subsequently deposited as voucher MUTPL M-18, the second confirmed record of the species for Ecuador. The record documents the occurrence of *L. brachyotis* in humid forest along the Andean–Amazonian interface.

3.6. Morphological and Taxonomic Validation

Morphological examination of voucher specimens from newly documented and selected previously reported localities confirmed their assignment to *L. brachyotis*. The species

has historically been placed in *Schizostoma*, *Micronycteris*, *Glyphonycteris*, and *Lampronnycteris*, and *M. platyceps* was described from Trinidad before being treated as a synonym of *L. brachyotis*. *Lampronnycteris* is currently treated as a monotypic genus, and identification therefore relies on distinguishing *L. brachyotis* from morphologically similar micronycterine bats using the combination of external, cranial, and dental characters described below [18,28,29]. This nomenclatural history made comparison with type-associated material particularly relevant for validating geographically important records. The examined specimens showed the diagnostic combination of separate, relatively short and pointed ears with a concave outer margin, absence of an interauricular band, a narrow and pointed noseleaf, paired smooth tubercles on the lower lip separated by a median groove, and yellow-orange to reddish coloration of the throat and upper chest [18,28,29]. Cranial and dental characters included an inflated rostrum, shallow basisphenoid pits, a relatively broad zygomatic region, visible upper outer incisors in lateral view, and trifold lower incisors [18,28,29]. Cranio-dental traits reported for the species include a low braincase, swollen rostrum and interorbital region, shallow basisphenoid pits, chisel-shaped upper inner incisors, bifid upper outer incisors, straight upper premolars, and a dental formula of $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3 = 34$ [18,28,29]. These characters were consistent across the physically examined material from Venezuela, Colombia, and Ecuador, and with the photographic documentation of the Trinidad type material. In particular, MUTPL M-18 from southern Ecuador and ICN 17238 from northern Colombia agreed with the diagnostic morphology observed in comparative specimens and in photographic documentation of the holotypes of *S. brachyote* and *M. platyceps* (Figure 5). External diagnostic features of MUTPL M-18, including the yellow-orange ventral pelage and the relative length of the calcar and foot, are shown in Figure 6.

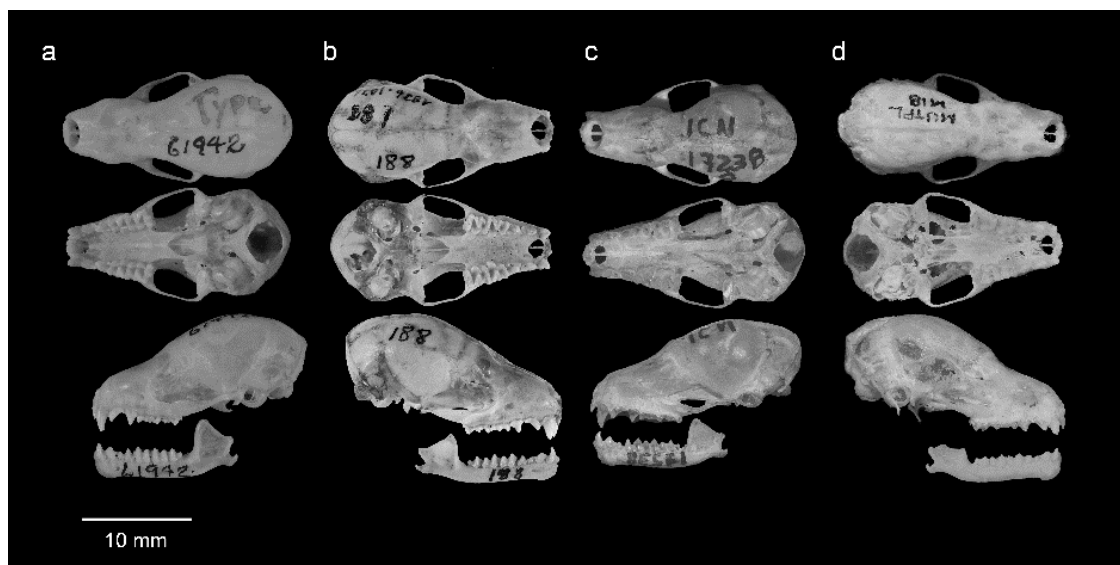


Figure 5. Comparative cranial morphology of selected specimens of *Lampronnycteris brachyotis* (Dobson, 1879). (a) FMNH 61942, holotype of *Micronycteris platyceps* Sanborn, 1949, Guanapo, Trinidad and Tobago; (b) MNHN-ZM-MO-1876-1074, holotype of *Schizostoma brachyote* Dobson, 1879, Cayenne, French Guiana; (c) ICN 17238, Pueblo Nuevo, Córdoba, Colombia; and (d) MUTPL M-18, Maycu, Zamora Chinchipe, Ecuador. Specimens are housed in the Field Museum of Natural History (FMNH), Chicago, IL, USA; the Muséum national d’Histoire naturelle (MNHN), Paris, France; the Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá, Colombia; and the Museo de Zoología, Universidad Técnica Particular de Loja (MUTPL), Loja, Ecuador, respectively. From top to bottom: dorsal, ventral, and lateral views. Scale bar = 10 mm.

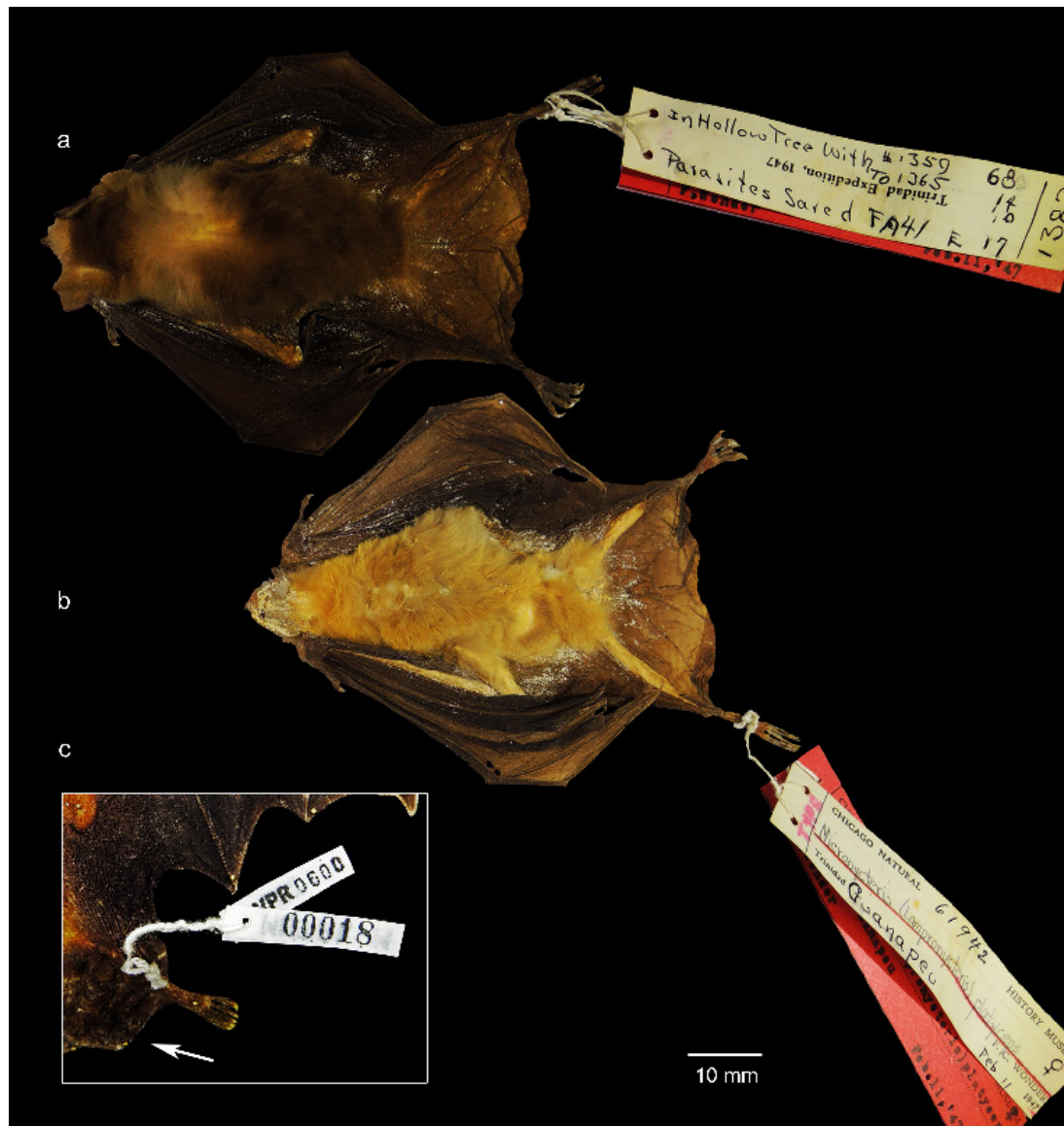


Figure 6. External appearance of preserved specimens of *Lampronycteris brachyotis* (Dobson, 1879). (a) Dorsal and (b) ventral skin views of the holotype of *Micronycteris platyceps* Sanborn, 1949 (FMNH 61942), from Guanapo, Trinidad and Tobago, collected by F. C. Wonder and housed in the Field Museum of Natural History, Chicago, IL, USA. (c) Inset showing calcar approximately as long as the foot in MUTPL M-18, the second confirmed record from Ecuador, collected by Víctor Romero at Maycu, Zamora Chinchipe, Ecuador, and housed in the Museo de Zoología, Universidad Técnica Particular de Loja, Loja, Ecuador. Note the characteristic yellow-orange ventral pelage. Scale bar = 10 mm.

Cranial and external measurements of the examined specimens fell within the comparative range summarized in Table 1, with no evidence of discrete morphological differentiation among the geographic regions represented.

Table 1. Selected external and cranial measurements of *Lamproncyteris brachyotis* specimens and comparative material.

Record	S	FA	CL	GLS	CBL	PL	ZB	MB	BBC	LPB	LMxT	GBM	GBC	Locality
EBRG 05043 ^a	M	41.3		20.59	18.79	10.07	10.72	9.81	8.9	5.04	4.06	–	–	Tamatama, Venezuela
EBRG 24358 ^a	F	42.3		21.12	19.33	10.65	10.81	9.82	8.83	5.22	4.49	9.08	3.95	Delta Amacuro, Venezuela
EBRG 24359 ^a	F	41.8		21.0	19.2	10.3	10.8	9.8	8.8	5.0	4.3	8.8	3.7	Delta Amacuro, Venezuela
EBRG 25644 ^a	F	40.9		20.64	18.56	10.03	10.2	9.55	8.9	5.06	–	8.44	3.25	Choroni, Venezuela
EBRG 28572 ^a	F	40.5		20.35	18.57	9.96	10.6	9.855	9.11	5.1	4.25	8.56	3.87	Bolivar, Venezuela
FMNH 61941 ^b	F	39.6		21.3	18.8	9.5	10.4	9.4	8.7	5.2	8.2	6.7	3.9	Guanapo, Trinidad
FMNH 61942 ^c	F	39.8		21.2	18.6	9.6	10.3	9.6	8.8	4.9	8.0	6.6	3.8	Guanapo, Trinidad
FMNH 61943 ^b	M	40.0		21.6	18.8	9.5	10.6	9.6	8.8	5.2	8.2	6.8	3.4	Guanapo, Trinidad
ICN10098 ^a	M	39.5		20.11	18.35	9.58	10.05	9.475	8.9	5.12	4.58	8.36	3.06	Restrepo, Meta, Colombia
ICN 12278 ^a	M	42.2		21.04	19.97	10.47	10.57	9.67	8.77	5.05	4.59	9.28	4.06	Tolima, Colombia
ICN 16955 ^a	F	39.3		20.81	18.86	10.28	10.33	9.57	8.81	4.93	4.2	8.95	3.83	Mitú, Vaupés, Colombia
ICN 17238 ^a	F	41.9		21.05	19.1	10.1	10.68	9.8	8.85	5.01	4.42	8.7	3.92	Córdoba, Colombia
MNHN 1876-1074 ^d	M		11.4	21.7	19.5		10.8	10.0	8.7	5.1	8.5	7.0	4.2	Cayenne, French Guiana
MUTPL M-18 ^e	F	39.9	11.2	21.4	18.7	9.6	10.3	9.5	8.6	5.1	8.2	6.7	3.69	Maycu, Ecuador
QCAZ 10749 ^f	M	39.8	11.6	21.7	19.6	9.5	10.7	–	8.9	4.9	8.4	6.5	2.7	Tarangaro, Ecuador
TTU 5237 ^g	F	39.4		21.3	18.5	–	10.2	–	8.6	5.0	8.1	6.7	–	Maracas Valley, Trinidad
TTU 5314 ^g	M	39.4		21.9	19.2	–	10.5	–	8.9	5.2	8.2	7.0	–	Blanchisseuse, Trinidad
TTU 5315 ^g	F	40.9		21.6	19.0	–	10.4	–	8.4	5.1	8.6	6.9	–	Blanchisseuse, Trinidad

Note: All measurements are in millimeters. Superscript letters indicate source or specimen status: a, this study; b, topotypical material reported by Sanborn [28]; c, Sanborn's holotype, FMNH 61942, holotype of *Micronycteris platyceps* Sanborn, 1949; d, Dobson's holotype, MNHN 1876-1074, holotype of *Schizostoma brachyote* Dobson, 1879; e, MUTPL M-18, second confirmed Ecuadorian record; f, QCAZ 10749, first Ecuadorian record [31]; g, comparative material. Abbreviations: FA, forearm length; CL, calcar length; GLS, greatest length of skull; CBL, condylobasal length; PL, palatal length; ZB, zygomatic breadth; MB, mastoid breadth; BBC, breadth of braincase; LPB, least postorbital breadth; LMxT, length of maxillary toothrow; GBM, greatest breadth across molars; GBC, greatest breadth across canines. En dash indicates unavailable data.

4. Discussion

The expanded occurrence dataset, specimen-based validation, and ecological niche models presented here refine the biogeographic interpretation of *L. brachyotis*. The documented distribution does not form a fully continuous pattern across all Neotropical forest systems, nor is it composed exclusively of deeply isolated records. It also does not show a pattern dominated only by deeply isolated fragments. The strongest signal is a coherent Amazonian-Guianan core with peripheral extensions into Central America, the Andean-Amazonian interface, northern Colombia, and mesic sectors of more open landscapes. This pattern suggests that the apparent fragmentation of the species' range reflects both real ecological filtering and incomplete documentation. The distribution of *L. brachyotis* should therefore be interpreted in light of the interactions among climatic suitability, historical forest dynamics, low detectability, and sampling bias.

4.1. Distributional Reassessment of *Lamproncyteris brachyotis*

Rocha et al. [23] framed *L. brachyotis* within the problem of Amazonian and Atlantic Forest disjunctions in South American forest-dwelling bats. Their study asked whether the scarcity of records across the dry diagonal reflected true biogeographic separation or sampling deficiency. Their models supported a strong association between *L. brachyotis* and forested environments, but also identified potential suitability in humid enclaves of northeastern Brazil. This combination is important because it did not portray the dry diagonal as uniformly unsuitable. The expanded and curated dataset assembled here revisits that hypothesis with a broader empirical base.

The new dataset gives greater weight to the northern part of the distribution. Reviewed records form a broad belt from Central America through Colombia, Venezuela, the Guiana Shield, and the Amazonian lowlands. This pattern supports an Amazonian-Guianan distributional core rather than isolated northern localities. The Central American and northern Andean records extend this core toward adjacent humid forest systems. The occurrence dataset, therefore, weakens a strictly disjunct interpretation across the species' range. The remaining discontinuities are most evident south of the Amazon basin.

Records south of the Amazon basin remain sparse and geographically scattered. Southeastern and central Brazilian records are best interpreted as peripheral records rather than as evidence of uninterrupted occupancy across intervening regions. The occurrence of *L. brachyotis* in Cerrado landscapes shows that the species can occur in mesic or forested environments embedded within more open formations [21]. Humid forest remnants may support peripheral populations beyond the main distributional core.

The Ecuadorian and Colombian records are especially informative because they affect mapped range limits. The specimen from Maycu confirms the presence of the species in southern Ecuador along the Andean-Amazonian interface. That record complements the first confirmed occurrence in Ecuador [31]. The Colombian record from Córdoba extends the species into a poorly represented sector of northern Colombia.

These new records do not prove continuous occupancy across all intervening areas. They show that verified museum material can change the perceived distribution of a rarely recorded species. They also show that range polygons can lag behind specimen-based evidence. This problem is common in Amazonian biodiversity, where collection effort remains biased, and many species distributions are incompletely documented [3,10]. The occurrence-based reassessment therefore provides the context needed to interpret the ecological niche models.

4.2. Climatic Suitability and Model Interpretation

The revised model showed consistent predictive performance under spatially structured evaluation. Because AUC is sensitive to background extent and should not be interpreted as a standalone measure of model quality, we considered it together with AUCdiff, CBI, OR10, AICc, and null-model comparisons [32,33]. Mean validation AUC was 0.685 ± 0.041 , with an AUCdiff of 0.044 ± 0.034 , a Continuous Boyce Index of 0.750 ± 0.085 , and an OR10 of 0.130 ± 0.076 . Importantly, the empirical model performed significantly better than the null-model expectation for validation AUC and CBI, indicating that its predictive performance exceeded that obtained from models fitted to random occurrence data under the same spatial evaluation framework.

Under current conditions, the model recovered broad but spatially heterogeneous climatic suitability across northern South America, including Colombia, Venezuela, the Guiana Shield, and northern Amazonia, where much of the documented occurrence evidence is concentrated. Suitable conditions also occurred in parts of Mesoamerica, the Andean–Amazonian interface, central Brazil, and southeastern Brazil. This geographic correspondence supports a broad northern South American climatic-suitability core, but it does not imply that all climatically suitable areas are occupied. Predictions beyond the main concentration of documented records should therefore be treated as hypotheses for future surveys rather than as evidence of realized distributions. Ecological niche models estimate environmental compatibility and do not directly measure occupancy, dispersal, population continuity, or gene flow [34]. Local forest structure, roost availability, and landscape configuration may further determine whether climatically suitable areas are actually occupied [35].

Temporal projections also showed substantial changes in the spatial configuration of climatic suitability while repeatedly recovering suitable conditions across Central America and northern South America. The mid-Holocene retained extensive suitable conditions across northern South America and much of Amazonia, the Last Glacial Maximum showed broad suitability across Amazonia and parts of the continental interior, and the Last Interglacial emphasized a more northerly configuration. Because the Last Glacial Maximum layers were spatially coarser than those used for the other scenarios, fine-scale differences should not be overinterpreted. More generally, these paleoclimatic projections allow us to evaluate how the spatial configuration of climatic suitability changed through time and whether those changes are compatible with biogeographic hypotheses of historical connectivity among forest regions. They do not, however, provide direct evidence of historical occupancy, continuous forest cover, realized dispersal corridors, or demographic continuity [36].

4.3. The Dry Diagonal as a Heterogeneous Ecological Filter

The South American dry diagonal, formed principally by the Caatinga, Cerrado, and Chaco, separates Amazonia from the Atlantic Forest and has often been interpreted as a barrier for forest-associated taxa [11,12]. Rocha et al. [23] placed *L. brachyotis* within this same biogeographic problem. Our occurrence data and climatic projections are consistent with heterogeneous ecological filtering across the dry diagonal, but they do not show that this region acts as a uniform or absolute barrier.

The region contains gallery forests, riparian corridors, humid enclaves, wetlands, semideciduous forests, and ecotonal habitats within broader open and seasonal formations. Records from the Cerrado demonstrate that *L. brachyotis* can occur in mesic or forested environments embedded in predominantly open landscapes [21]. Rocha et al. [23] also predicted suitable conditions in humid enclaves of northeastern Brazil. These observations

indicate local habitat availability, but they do not establish continuous occupancy across the dry diagonal.

The Pantanal provides a useful ecological comparison. Bat assemblages in this savanna-wetland system include Amazonian, Cerrado, Chaco, and Atlantic Forest influences, while many phyllostomids remain associated with forested habitats within the surrounding matrix [37]. This pattern shows that open regions can contain local environments relevant to forest-associated bats. It does not demonstrate that *L. brachyotis* currently disperses across the Pantanal or other sectors of the dry diagonal [38]. The ecological effect of the dry diagonal probably varies with the amount, arrangement, and structural quality of forested habitat [35]. The close association of *L. brachyotis* with forest structure supports this interpretation [22]. Gallery forests and humid enclaves may permit local occurrence, whereas extensive open formations may reduce habitat availability. Because forest configuration and connectivity were not modeled directly, these mechanisms remain hypotheses. The dry diagonal is therefore best interpreted as a region of variable ecological permeability rather than as either an absolute barrier or a continuous corridor.

4.4. Historical Connections Between Amazonia and the Atlantic Forest

The distribution of *L. brachyotis* should be interpreted within the complex biogeographic relationship between Amazonia and the Atlantic Forest [39]. Ecological niche models developed for rainforest taxa have recovered several potential Last Glacial Maximum routes of climatic connection rather than a single continuous corridor [13]. This evidence favors a spatially heterogeneous historical framework, but climatic routes modeled for other taxa cannot be assumed to have been occupied by *L. brachyotis*. Our temporal projections showed broad climatic suitability during the Last Glacial Maximum across Amazonia and parts of the continental interior. This pattern indicates that climates compatible with the modeled niche may have been more widely distributed during that period. It does not demonstrate continuous humid forests or a functional dispersal corridor. The coarser spatial resolution of the Last Glacial Maximum layers and the potential effects of environmental extrapolation further limit fine-scale historical interpretation.

Palaeoecological evidence likewise indicates that South American seasonally dry forests had regionally heterogeneous histories of expansion, replacement, and persistence during the Late Quaternary [14]. Peripheral suitable areas may therefore have had different historical meanings in different regions. The repeated recovery of favorable climatic conditions in the Guiana Shield and northern Amazonia coincides geographically with the concentration of documented records that defines the Amazonian-Guianan core of the known distribution. It does not demonstrate that this region functioned as a single refugium or remained demographically continuous through time. The apparent Amazonian-Atlantic Forest disjunction in *L. brachyotis* is therefore best treated as a composite pattern. Climatic change may have altered dispersal opportunities, local mesic habitats may have supported peripheral occurrences, and incomplete sampling may have exaggerated some gaps. The available evidence does not distinguish among long-term isolation, intermittent connection, and overlooked populations. Resolving these alternatives will require phylogeographic data and habitat-based analyses.

4.5. Wallacean Shortfall, Detectability, and Sampling Bias

The Wallacean shortfall [3] remains central to interpreting *L. brachyotis*. Species-occurrence data are geographically and temporally biased [5], particularly in tropical regions where collecting is concentrated near accessible localities, protected areas, roads, rivers, and historically active institutions. For rarely recorded species, these biases can create apparent gaps that resemble biogeographic discontinuities [40].

Lampronnycteris brachyotis is rarely captured in Neotropical bat inventories, but low capture frequency is not a direct estimate of population size. Ground-level mist nets can underrepresent bats that use forest interiors, particular flight paths, or higher vertical strata [15]. The species' specialized foraging behavior and association with forest structure may also make detection sensitive to net placement, vegetation structure, season, and survey duration [20,22]. Nondetection during a short or methodologically restricted inventory therefore provides weak evidence of true absence. Sampling bias also affects ecological niche models. Incomplete occurrence data can emphasize well-sampled environments and omit poorly documented portions of a species' niche. Model evaluation is also influenced by geographic extent, background definition, and the distribution of evaluation data, which limits the interpretation of AUC as a standalone measure of model quality [33].

Spatially structured evaluation and restriction of the background to the accessible area reduced some sources of bias in this study, but they could not fully compensate for gaps in the occurrence record. The model should consequently guide surveys rather than define hard range limits. Suitable areas without records may contain overlooked populations, but they may also lack habitat conditions not represented by the climatic predictors. Conversely, poorly sampled regions should not be treated as confirmed absences. The strongest evidence supports a coherent Amazonian-Guianan core and several verified peripheral extensions. Remaining discontinuities should be treated as hypotheses produced by some combination of ecological filtering and incomplete observation.

4.6. Taxonomic Reliability and Museum Evidence

Taxonomic reliability is essential to the biogeographic interpretation of *L. brachyotis*. A misidentified peripheral record can alter range maps and ecological niche models, whereas a verified specimen can correct an underestimated distribution. This is especially important because the species has been placed in *Schizostoma*, *Micronycteris*, *Glyphonnycteris*, and *Lampronnycteris*, and the Trinidadian taxon *Micronycteris* (*Lampronnycteris*) *platyceps* was subsequently treated as a synonym of *L. brachyotis* [18,28,29]. Historical names and records must therefore be associated with a consistent taxonomic concept.

The specimen-based comparisons conducted here provide the foundation for the most geographically informative records. Selected vouchers from Venezuela, Colombia, and Ecuador were compared with published descriptions, morphometric evidence, and photographs of the holotypes of *S. brachyote* and *M. (L.) platyceps*. The examined material showed the diagnostic external and cranial combination of *L. brachyotis*, and its measurements fell within the documented range of variation [18,28,29]. No discrete morphological discontinuity was observed among the specimens compared.

MUTPL M-18 from southern Ecuador and ICN 17238 from northern Colombia are particularly important because they document peripheral occurrences, supported by vouchers, locality data, and diagnostic morphology. MUTPL M-18 represents the second confirmed record for Ecuador and complements the first national record, QCAZ 10749 [31]. Their inclusion strengthens the distributional reassessment without implying continuity across intervening areas.

Taxonomic support is not uniform across the complete dataset. Some locality units are based on specimens examined in this study, whereas many others depend on published identifications that could not be reassessed directly. All records were reviewed for geographic and taxonomic consistency, but literature-only records remain contingent on their original documentation. Museum collections are therefore central to reliable distributional inference because they preserve diagnostic material, labels, historical evidence, and tissues for future analyses. This role is especially important in South America, where collections

remain affected by uneven digitization, infrastructure limitations, staffing constraints, and restricted access to some comparative material [9].

4.7. Conservation and Future Research

New voucher-based records from southern Ecuador and northern Colombia, along with other peripheral occurrences, show that the current map does not encompass the complete documented distribution and should be considered in future updates. These records identify the Nangaritza region in southern Ecuador, the Córdoba locality in northern Colombia, and other peripheral sectors as priorities for targeted surveys, but they do not establish population continuity or conservation status.

Future inventories should address detectability directly. Surveys should include forest interiors, riparian environments, potential roosting sites, and vertical strata above ground level. Complementary methods and repeated sampling are needed because standard ground-level mist-netting may underestimate rarely recorded forest bats [16]. Survey design should also reflect the species' association with forest structure and specialized foraging behavior [22].

Future models should incorporate finer-scale habitat information. Climatic predictors cannot resolve canopy structure, forest continuity, gallery forests, roost availability, or local matrix quality. Remote-sensing layers could test whether climatically suitable areas also contain habitat conditions compatible with occurrence. Phylogeographic data are likewise needed to determine whether peripheral records represent historical isolation, intermittent dispersal, or overlooked components of a broader distribution. Continued examination and digitization of museum collections should accompany new field surveys. Historical specimens can reveal overlooked records, permit taxonomic reassessment, and provide tissues for molecular studies. The main conservation contribution of the present study is therefore a more reliable representation of geographic evidence, not a reassessment of extinction risk.

5. Conclusions

The 125 documentary and specimen records compiled in this study, consolidated into 121 unique locality-coordinate units, support a coherent Amazonian-Guianan core of the documented distribution of *L. brachyotis* and several peripheral extensions. The voucher-based records from southern Ecuador and northern Colombia fall outside the current IUCN range polygon and show that the documented distribution remains incomplete along its margins. They do not establish continuous occupancy across intervening regions.

The climatic model, calibrated with 115 unique presence cells, recovered broad but spatially heterogeneous suitability across northern South America, with additional suitable areas in Mesoamerica, the Andean–Amazonian interface, central Brazil, and southeastern Brazil. Temporal projections identified recurrent areas of climatic suitability in northern South America, but they do not demonstrate historical occupancy, continuous forest cover, or demographic continuity. The dry diagonal is therefore best interpreted as a region of variable ecological permeability rather than as a uniform barrier.

The apparent fragmentation of *L. brachyotis* probably reflects the combined influence of habitat heterogeneity, climatic variation, low detectability, and uneven sampling. Specimen-based validation is essential because individual peripheral records can substantially alter range maps and biogeographic interpretations. Targeted surveys, finer-scale habitat analyses, and phylogeographic data are required to resolve the status and history of peripheral populations.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18090525/s1>. Supplementary Figure S1: Pairwise Pear-

son correlation matrix for the eight bioclimatic predictors retained for ecological niche modeling of *Lamproncycteris brachyotis*. Correlations were calculated across the calibration area. No retained pair exceeded the predefined collinearity threshold of $|r| = 0.70$; the highest absolute correlation was between BIO13 and BIO19 ($r = 0.671$). Supplementary Dataset S1: Occurrence records and unique locality-coordinate units of *L. brachyotis* used in the distributional reassessment and ecological niche modeling. The workbook contains 125 occurrence/documentary records and 121 unique locality-coordinate units, together with dataset-level metadata, a data dictionary, and a quality-control summary. Of the 121 locality units, five were excluded because environmental data were missing, leaving 116 environmentally valid localities; after cell-level deduplication, 115 unique presence cells were used for model calibration. Catalog number and institution information are reported only when documented in the compiled dataset; blank fields should not be interpreted as evidence that no voucher exists.

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Institutional Review Board Statement: Not applicable. The present study relied primarily on museum specimens, associated collection metadata, and published occurrence records and did not involve any new field collections or experimental procedures. Specimen MUTPL M-18 was not collected specifically for this article; it was collected previously under research permit No. MAE-DNB-CM-2015-0016, transported under mobilization guide No. UPN-VS-GM-066-2018, and deposited in the Museo de Zoología, Universidad Técnica Particular de Loja (MUTPL), Loja, Ecuador, in accordance with the legal requirements of the relevant Ecuadorian authorities.

Data Availability Statement: The occurrence data and associated metadata supporting the distributional analyses are provided in Supplementary Dataset S1. Appendix A presents a formatted summary of the 121 unique locality-coordinate units. Additional specimen-associated information is available from the corresponding natural history collections, subject to their respective access policies. Ecological niche modeling outputs are available from the corresponding author upon reasonable request.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Gazetteer of Reviewed Unique Locality-Coordinate Units of L. brachyotis (Dobson, 1879)

Localities are arranged alphabetically by country and first-level administrative division. Coordinates are reported in decimal degrees under the WGS 84 datum and rounded to four decimal places; negative values indicate southern latitudes and western longitudes. Voucher numbers are provided when documented. Institutional acronyms are as follows: EBRG, Estación Biológica de Rancho Grande, Maracay, Venezuela; FMNH, Field Museum of Natural History, Chicago, IL, USA; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; MNHN, Muséum national d'Histoire naturelle, Paris, France; MUTPL, Museo de Zoología de la Universidad Técnica Particular de Loja, Loja, Ecuador; and Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador. An asterisk indicates a locality excluded from ecological niche modeling due to missing environmental data.

BELIZE. Cayo: Cave at 1 km NW Augustine, 16.9669, −89.1331 [41]. Orange Walk: Lamanai, 17.8914, −88.6714 [42]. Stann Creek: May Flower-Bocawina National Park, 16.97, −88.4858 [43].

BOLIVIA. Cochabamba: Cavernas de Repechón, Parque Nacional Carrasco, −17.1667, −65.5417 [44]. Santa Cruz: Bosque Experimental Elías Meneses, Yapacaní, Ichilo, 209 Km NW of Santa Cruz de la Sierra, −16.5592, −64.36972 [45].

BRAZIL. Acre: Senador Guimard, −10.1, −67.65 [46]; Fazenda Experimental Catuaba, Senador Guimard, 25 km from Rio Branco, −10.1194, −67.6778 [46]. Amapá: Rio Curiaú, Macapá, 0.1667, −50.9833 [47]; Reserva de Desenvolvimento Sustentável do Rio Iratapuru, −0.4, −52.5 [48]. Amazonas: 80 km north from Manaus, Maranhão, −2.4, −59.72 [49]; Reserva de Desenvolvimento Sustentável Amanã, −2.4167, −64.75 [50]. Bahia: Una região, Southern Bahia, −15.3833, −39.1528 [51]. Espírito Santo: Estação Experimental de Linhares, Linhares, −19.3833, −40.05 [52]; Lago da Administração, Reserva Natural Vale, Linhares, −19.1594, −40.1106 [53]. Mato Grosso: Médio Teles Pires, −10.9778, −55.8139 [54]; Nova Canaã do Norte, −10.9986, −55.75 [54]; Comodoro, −13.85, −60.35 [21]; APA Cabeceiras do Rio Cuiabá, Rosário Oeste, −14.46611111, −55.88 [55]; Sesc Serra Azul, Cabeceiras do Rio Cuiabá, −14.48333333, −55.73611111 [55]; Barra do Garças, Barra do Garças, −15.4831, −52.3661 [56]; Serra Azul State Park, Barra do Garças, −15.9042, −52.29 [56]. Pará: Guamá, Belém, −1.45, −48.25 [57]; Parque Nacional Montanhas do Tumucumaque, −1.9472, −52.8111 [48]; Alter do Chão, Tapajós River, 40 km from Santarém, −3.0006, −55.0239 [58]; Floresta Nacional dos Tapajós, −3.35, −54.95 [59]; Igarapé Brabo, on the Tapajós river, −2.4333, −55 [60]; Parque Nacional da Amazônia, near Santarém, and 54 km south of Itaituba, −2.5469, −54.8428 [61]; Lower Xingu River, Altamira, −3.2, −52.2 [21]. Floresta Nacional dos Carajás, −6.3161, −50.7 [48]. Paraná: Trilha da Samambaia, Reserva Natural Morro da Mina, −25.5747, −48.9153 [62]. Rondônia: Porto Velho, −10, −65 [21]. São Paulo: Parque Estadual Serra do Mar, −23.5833, −45.4167 [63]; Estação Ecológica Juréia, Itatins, −24.4, −47.1 [21]; Gruta São José do Ribeira, −24.53333, −48.3 [64]; Pedro Cubas, Eldorado Paulista, −24.65, −48.3 [64]; Ilha do Cardoso, −25, −48 [21].

COLOMBIA. Arauca: El Colachero, Cravo Norte, 6.4064, −69.7789 [65]. Bolívar: Cartagena de Indias*, 10.4867, −75.6169 [41]; Cantagallo, 7.1564, −74.3289 [66]. Caldas: Norcasia, Reserva Natural Río Manso, 5.6894, −74.8322 [67]; La Samaná, Cuenca media del Río la Miel, 5.42917, −75.02778 [68]; Samaná, 5.4281, −75.0486 [67]. Caquetá: Serranía de Chiribiquete, SE río Mesay, Puerto Abeja, 0.1417, −72.4639 [65]. Casanare: Hato Corozal, caño Yaguarapo, 6.3395, −71.6383 [65,69]; Paz de Ariporo, río Ariporo, 6.2087, −70.2107 [69]; Támara, 5.8295, −72.2403 [70]; Volcán Blanco, 5.4472, −72.5667 [71]; Hato el Boral, San Luis de Palenque 165 msnm, 5.4028, −71.8994 [65]; Las Delicias, Aguazul, 4.87, −72.5347 (iNaturalist, submitted by Darwin Morales. Available in (<https://www.inaturalist.org/observations/742550>, accessed on 5 July 2026). Córdoba: Pueblo Nuevo, Hacienda Praga, 8.5506, −75.4269 (ICN 17238; this study). La Guajira: Nasaret, 12.1833, −71.2833 [72]. Meta: Restrepo, bocatomía Caney Alto, 4.3331, −73.585 (ICN 10098; this study); La Macarena, Cascada de Los Cuarzos, 2.3003, −73.8583 [73]. Santander: Puerto Wilches, 7.365, −73.8286 [65]. Tolima: Maríquita, 5.3325, −74.9511 (ICN 12277; ICN 12278; this study). Vaupés: Mitú, 1.2678, −70.3456 (ICN 16955; this study); Durania, 1.2667, −70.1833 [72]. Vichada: Puerto Carreño, isla fluvial Santa Helena, 6.1166, −67.4706 [73]. COSTA RICA. Guanacaste: Finca La Pacífica, 4 km NW Cafías, 10.4667, −85.15 [74]; Rafael Rodríguez Wildlife Refuge, Palo Verde, 10.3872, −85.3483 [41]; Heredia: La Selva Biological Station, 10.5611, −84.0333 [75]; Puntarenas: La Gamba Biological Field Station, 8.71694, −83.2269 [76].

ECUADOR. Pastaza: Tarangaro near to the Manderoyacu River, −1.4089, −77.5292 (QCAZ 10749; this study; [31]). Zamora Chinchipe: Maycu, Nangaritza, −4.2939, −78.6969 (MUTPL M-18; this study).

FRENCH GUIANA. Cayenne: Cayenne, 4.9789, −52.4801 (MNHN-ZM-MO-1876-1074; [77]).

GUATEMALA. Petén: Chuntuqui, 17.66, −90.1531 [78]; Tikal National Park, 17.35, −89.7 [79].

GUYANA. Potaro-Siparuni: Iwokrama Forest, Pakatau Falls, 4.75, −59.0169 [80].

MEXICO. Campeche: Hapolol, 20.0167, −90.4667 [81]; Calakmul, Banqueta, 18.8833, −89.35 [82]; Calakmul, Campeche, 18.4167, −90 [81]; Calakmul, Central Chiklera Villa Hermosa, 18.0333, −89.7361 [82]. Chiapas: Florida, 50 Km E to Altomirano, 16.7433, −92.6231 [83]; Lacandona, 16.0667, −90.75 [84]; Motozintla, 15.2667, −92.4169 [85]. Oaxaca: Mazahuito, 16.7458, −94.973 [86]. Quintana Roo: Tuzik, Espita, Península Yucatán, 21.2022, −88.46028 [87]; Tulum, 20.2511, −87.52528 [88]; Reserva Sian Káan, Península de Yucatán, 19.5833, −87.7167 [89]. Tabasco: Agua Blanca State Park, 17.6167, −92.4669 [90].

NICARAGUA. Chinandega: Volcán de Chinandega, 12.80638889, −87.12638889 [28]. Rivas: Rivas, 11.5211, −85.9003 (iNaturalist, submitted By Yuri Aguirre. Available in <https://www.inaturalist.org/observations/652980>, accessed on 5 July 2026); Paso del Itmo, Tola, 11.3469, −85.8222 (iNaturalist, submitted by Jose Martinez. Available in <https://www.inaturalist.org/observations/402330>, accessed on 5 July 2026).

PANAMA. Colón: Parque Nacional Soberanía, Bella Vista, 9.325, −79.9272 [22]; Fort Sherman Military Reservation, 3 km W Cristobal, 9.3333, −79.95 [74]. Los Santos: Jobero, 7.3719, −80.5953 [41]. Panama: Cerro Azul, 9.3806, −79.4872 [41]; Naval Ammunition Depot, 8 km W Balboa, 8.95, −79.6167 [74]. Veraguas: Isla Cébaco, Montijo, 7.6414, −81.1744 [41].

PERU. Huánuco: Panguana Biological Station, Huiinuco, Yuya Pichis river, −9.6167, −74.9333 [91]. Loreto: Maynas, Campamento Catalino, Río Lagartococha, Torres Causana, −0.5806, −75.3194 [92]; Requena, Centro de Investigaciones Jenaro Herrera, 2.5 km E Ucayali river, 140 km SSW Iquitos, −4.9558, −74.0103 [92]; Maynas, Indiana, Yanamono, Quebrada Yanamono, aprox 60 km NE Iquitos, −3.5861, −72.9361 [92]; Requena, Yaquerana,

Nuevo San Juan, Río Gálvez, −5.25, −73.1669 [92]. Madre de Dios: Cocha Juárez, Madre de Dios river, Manu Biosphere Reserve, −12.2083, −71.2139 [93].

SURINAM. Brokopondo: Gros, 5.1, −55.1833 [94].

TRINIDAD AND TOBAGO. Couva-Tabaquite-Talparo: Couva, 10.41667, −61.45 [95]. Penal-Debe: Penal, Trinidad, 10.1767, −61.4653 [95]. Río Claro-Mayaro: Mayaro, 10.5367, −61.1014 [96]; Guayaguayare, 10.2, −61.0667 [97]; Victoria-Mayaro Forest Reserve, 10.1667, −61.3331 [20]. Siparia: Buenos Ayres*, 10.2336, −61.7283 [95]; Siparia, Trinidad, 10.2056, −61.6306. Tunapuna-Piarco: Blanchisseuse*, 10.9333, −61.3 [98,99]; Brasso Seco*, 10.895, −61.3997 [99]; Maracas Valley*, 10.8039, −61.5292 [98]; Guanapo, 10.7, −61.3611 (FMNH 61942; [28]; this study).

VENEZUELA. Amazonas: Tamatama, Río Orinoco, 3.16667, −65.8169 (EBRG 05043; this study; [100]); Neblina Base Camp, Rio Mawarinuma, 0.95, −66.2 [101]. Aragua: Hacienda La Sabaneta, Choroní, 10.4667, −67.6167 (EBRG 25643; EBRG 25644; this study). Bolívar: Isla La Tigra, Río Caroní, 7.9725, −63.0875 (EBRG 28544; this study); Isla en Río Caroní, 1.5 Km aguas abajo Río Claro, 7.93, −63.1428 (EBRG 28572; this study); Los Patos, 25 km SE El Manteco, 7.35138889, −62.43583333 [100]; Campamento Caurama sector el Tapón, Maripa, 7.33888889, −65.27777778 (EBRG 24522; this study); 28 km SE El Manteco, 7.33111111, −62.31805556 [41]. Delta del Orinoco: Isla Tobejuba, costa atlántica Boca del Caño Aragua, Reserva de Biosfera Delta del Orinoco, 9.44777778, −60.93222222 (EBRG 24359; this study); Isla Tobejuba, Caño Aragua, frente a la Comunidad Muaina, Reserva de Biosfera Delta del Orinoco, 9.34861111, −61.01 (EBRG 24358; EBRG 26523; EBRG 26524; this study). Sucre: 40 km NW of Caripito, 10.39611111, −63.47388889 [102]; Neverí Valley, SW Cumanacoa, 10.32833333, −64.14666667 [28]. Yaracuy: 19 km NW of Urama, 10.71722222, −68.54277778 [100]; Mayorica, Yurubí National Park, San Felipe, 10.43333333, −68.66666667 [103].

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