Phyllostomid Bats as a Model to Test Zoogeographic Units in Ecuador

Chapter · October 2019

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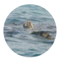

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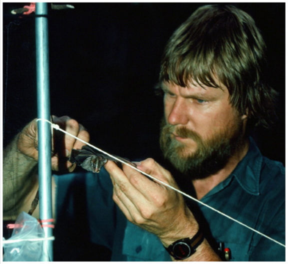


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Front cover: A selection of photos representing Robert J. Baker's career. The editors of this volume sincerely thank the many colleagues, friends, and students of Robert J. Baker that contributed 300+ photographs for the Baker retirement celebration in 2015 and for the memorial service in 2018, from which the images featured on this cover were selected.

Top row, left to right: Baker in his Biology lab, 2006, photo by Neal Hinkle, courtesy of Texas Tech University; preparing to karyotype a *Sundamys muelleri*, Sabah, Malaysian Borneo, 2006, photo by Peter A. Larsen; pinning bat specimens, Rattlesnake Canyon, Val Verde County, Texas, 2005, photo by Bill D. Mueller, courtesy of Museum of Texas Tech University.

Middle row, left to right: examining a *Macrotus californicus*, 2011, Picacho Peak State Park, Arizona, photo by Lizette Siles; setting a mist net, 2009, Placitas, New Mexico, photo by Lizette Siles; removing a *Uroderma bilobatum* from a mist net, 1977, Guatemala, photo by Ira F. Greenbaum.

Bottom row, left to right: admiring a *Hipposideros galeritus*, Sarawak, Malaysian Borneo, 2006, photo by Peter A. Larsen; karyotyping, Guatemala, 1977, photo by Ira F. Greenbaum; with Chernobyl specimens at NSRL, 1990, photo by Artie Limmer, courtesy of Texas Tech University.

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Museum of Texas Tech University

Number 71

From Field to Laboratory: A Memorial Volume in Honor of Robert J. Baker

Edited by

Robert D. Bradley, Hugh H. Genoways, David J. Schmidly, and Lisa C. Bradley

Layout and Design: Lisa Bradley
Cover Design: Lisa Bradley; photos courtesy of various individuals (see inside front cover)
Production Editor: Lisa Bradley

This book was set in Times New Roman and printed on acid-free paper that meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

Printed: 11 October 2019

Library of Congress Cataloging-in-Publication Data

Special Publications of the Museum of Texas Tech University, Number 71
Series Editor: Robert D. Bradley

From Field to Laboratory: A Memorial Volume in Honor of Robert J. Baker

Robert D. Bradley, Hugh H. Genoways, David J. Schmidly, and Lisa C. Bradley (editors)

ISSN 0149-1768
ISBN 1-929330-37-5
ISBN13 978-1-929330-37-9

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(806)742-2442

PHYLLOSTOMID BATS AS A MODEL TO TEST ZOOGEOGRAPHIC UNITS IN ECUADOR

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ABSTRACT

Nine Zoogeographic Units (ZU) have been hypothesized for Ecuador, with seven of these units located within the continental portion of the country. Each ZU was defined by climate, topography, elevation, and vegetation type. In spite of their historical application, the validity of ZUs has not been tested. The goal of the present study was to treat the ZUs as hypotheses and test their validity. For this purpose, species of the bat family Phyllostomidae were used as a model. A total of 13,262 validated bat records, representing 109 species and six feeding guilds (with confirmed taxonomic identifications and geographic information), were analyzed using multivariate statistical analyses and geographic modeling. Results obtained from the Multidimensional Scaling Analysis, Detrended Correspondence Analysis, and Pairwise comparisons provided evidence that the ZUs as proposed were valid, based on information from phyllostomid bats, although no species was restricted to the Temperate Forests and High Andes. In addition, geographic models showed that Tropical Eastern Forests and Subtropical Eastern Forests were the most likely areas to be inhabited by phyllostomids. Bat species in the High Flying Frugivore and Insecti-Carnivore trophic guilds displayed a clear spatial pattern highly related to ZUs. The findings of this study provide important information regarding the validity of these ZUs for establishing priorities concerning research, conservation, and management in this group of mammals.

Key words: bats, Chiroptera, Ecuador, geographic distribution, Phyllostomidae, zoogeography

RESUMEN

En Ecuador se han propuesto nueve pisos zoogeográficos con siete de estas unidades localizadas en la porción continental del país. Cada piso zoogeográfico fue definido por su clima, topografía, elevación, y tipo de vegetación. A pesar de su aplicación histórica, la validez de estos pisos no ha sido puesta a prueba. El objetivo de este estudio fue tratar a los pisos zoogeográficos como hipótesis y evaluar su validez. Para este propósito, especies de la familia de murciélagos Phyllostomidae fueron utilizadas como modelo. Un total de 13,262 registros de murciélagos validados, representando a 109 especies y seis gremios tróficos (con identificación taxonómica e información geográfica confirmada) fueron analizados utilizando análisis estadísticos multivariados, y modelamiento geográfico. Los resultados obtenidos del Análisis de Escalamiento Multidimensional, Análisis de Correspondencia Sin Tendencia, y de Comparaciones por Pares, proporcionaron evidencias que soportan que los pisos zoogeográficos como están propuestos son válidos utilizando filostómidos. Aunque el Piso Templado y el Piso Altoandino no resgistran ninguna especie. Adicionalmente, los modelos geográficos mostraron que los Pisos Tropical Oriental y Subtropical Oriental fueron las áreas con más probabilidad para ser habitadas por los murciélagos filostómidos. Las especies de murciélagos de los gremios tróficos frugívoros de dosel y los insecto-carnívoros mostraron un patrón espacial altamente relacionado con los pisos zoogeográficos. Los resultados de este estudio proveen información importante relacionada a la validez de los pisos zoogeográficos para el establecimiento de prioridades relacionadas con la investigación, conservación, y el manejo en este grupo de mamíferos.

Palabras clave: distribución geográfica, Ecuador, murciélagos, Phyllostomidae, Quiróptera, zoogeografía

INTRODUCTION

More than 1,500 species of mammals inhabit the Neotropics (Patterson and Costa 2012). This remarkable amount of speciation and diversity represents approximately 30% of extant mammals (Wilson and Reeder 2005) and includes newly described species (Reeder et al. 2007; Gardner 2008a; Patterson and Costa 2012; Patton et al. 2015; Moras et al. 2018). The Tropical Andes region of northern South America, which includes Ecuador, constitutes an important area in terms of biodiversity, endemism, scientific research, and conservation efforts (Dodson and Gentry 1991; Mittermeier et al. 1998; Myers et al. 2000; Rodríguez-Mahecha et al. 2004a, 2004b; Marchese 2015).

Patterns of biodiversity in this geographic area seem to have been influenced directly by a complex association of orographic, climatic, and geological factors (Montgomery et al. 2001; Richter et al. 2008; Anderson et al. 2011). Historically, this complexity has made it difficult to characterize, classify, and define life zones, ecoregions, and biogeographic units within this biologically diverse region (Albuja-V et al. 2012). The definition and establishment of such categories is crucial in setting priorities and planning research activities and conservation strategies at a global or regional scale, in planning effective natural resource management policies, or simply visualizing the geographic distribution of certain species or species assemblages in a defined region (Olson et al. 2001; Corace et al. 2012; Solari et al. 2012). However, abiotic features, such as elevation, have a different effect on the dispersion of birds, bats, and rodents (Patterson et al. 1996, 1998; Kattan et al. 2004). Furthermore, some of the standard biological datasets, including those deposited in natural history museums, are incomplete, which in turn makes it difficult to avoid bias in quantifying biodiversity. This issue also is confounded by the differing opinion of experts regarding the number of species recognized from the region. Systematic revisions published over the last decade have revealed the presence of cryptic species and undescribed species (i.e., Baker et al. 2009; Larsen et al. 2012; Velazco and Patterson 2013, 2014, 2019), most of which have not been included in recent studies. Further, Baker and Bradley (2006) and Reeder et al. (2007) indicated that the number of mammalian species is underestimated by about 40%. Thus, it has been difficult to estimate biodiversity.

In 1892, Theodore Wolf published *Geography and Geology of Ecuador*, which has been recognized as the first treatment on topography, natural formations, geology, climatology, and political geography of the country. Based on categories of vegetation, Wolf divided Ecuador into five regions: dry coastal forests, wet coastal forests, humid Andean forests, inter-Andean forests (valleys), and the high Andes (including paramo). Later, Chapman (1926) identified four life zones for birds, based on vegetation type and elevation: tropical, subtropical, temperate, and páramo. In Chapman's classification, the tropical and subtropical life zones were subdivided into Pacific and Amazonian divisions, and the Pacific Tropical division was further divided into humid and dry regions. Chapman's classification included previous observations of the bird fauna from Colombia (Chapman 1917) and established similarities based on previous studies by Wolf (1892).

Cabrera and Yépez (1940) in their book *Mamíferos Sudamericanos* partitioned South America into eleven zoogeographic provinces. The area corresponding to Ecuador included seven zoogeographic provinces: Galápagos, Pacific, Amazon, Arid, Yungas, High Andes, and Páramo. Subsequently, Hershkovitz (1958, 1969), based on geographic distribution of mammals across the Neotropical region, established four sub-regions: Brazilian subregion (including Middle

American and South American portions), Patagonian, West Indies, and Holarctic. He concluded that Ecuador is a confluence point between the Brazilian subregion and the Patagonian subregion.

Albuja et al. (1980) used elevational ranges to redefine the life zones of Chapman (1926). The elevational increments proposed by Albuja et al. (1980) were developed based on distributions of species of fish, reptiles, amphibians, birds, and mammals known to occur in Ecuador. The inclusion of elevation resulted in the formal recognition of eight distinct ecoregions for the country (Table 1): Tropical Northwestern Forests, Tropical Southwestern Forests, Subtropical Western forests, Temperate Forests, High Andes, Subtropical Eastern Forests, Tropical Eastern Forests, and Galápagos Islands. The classification proposed by Albuja et al. (1980) is considered as a geographic hypothesis for the distribution of Ecuadorian mammals (i.e., Albuja 1999; Tirira 1999; Anderson and Jarrín-V 2002; Anderson and Martínez-Meyer 2004; Albuja and Gardner 2005; Griffiths and Gardner 2008; Tirira et al. 2011; Palacios et al. 2018).

More recently, Solari et al. (2012) revisited previous classifications, including Hershkovitz' (1958, 1969) studies of geographic distributions, that incorporated > 900 species of endemic mammals. Those distributions were allocated by Solari et al. (2012) into 11 subregions following the system proposed by Cabrera and Willink (1980) for the Neotropics. The subregions including Ecuador are the Choco, Andes, and Amazonian lowlands.

Despite these previous studies, a formal assessment to examine the validity of this zoogeographic classification, for specific taxonomic groups, has not been completed. The order Chiroptera constitutes the most diverse, collected, and studied group of mammals in Ecuador (see Albuja 1999; Tirira 2007; Burneo and Tirira 2014; Tirira 2017) and provides an ideal taxonomic group for testing the usefulness of zoogeographic classifications. Several new species have been described in the last two decades (i.e., *Anoura fistulata* Muchhala et al. 2005; *Micronycteris giovanniae* Fonseca et al. 2007; *Lonchophylla fornicata* Woodman 2007; *Eumops wilsoni* Baker et al. 2009; *Myotis diminutus* Moratelli and Wilson 2011; *Sturnira perla* Jarrín-V. and Kunz 2011; *Sturnira bakeri* Velazco and Patterson 2014; *Cynomops tonkigui* Moras et al. 2018; and *Molossus fentoni* Loureiro et al. 2018). These new discoveries suggest that the study and understanding of bat biodiversity in the Neotropics, specifically in the Northern Andes, remains incomplete for several bat faunas and reinforces the need to continue studying, surveying, and protecting these ecosystems. In recent decades, the study of bats in Ecuador has been the subject of increasing attention by researchers interested in their ecology, diversity, evolution, and conservation (i.e., Albuja 1982, 1999; Reid et al. 2000; Muchhala and Jarrín-V 2002; Larsen et al. 2010; Burneo and Tirira 2014).

Table 1. Zoogeographic units (ZUs) proposed for Ecuador by Albuja et al. (1980).

Zoogeographic Unit	Acronym	Area	Elevation Range
Galápagos	GAL	7,850 km²	0–1,607 m
High Andes	HA	29,092 km²	> 3,000 m
Subtropical Eastern Forests	SEF	19,928 km²	1,000–2,000 m
Subtropical Western Forests	SWF	15,579 km²	1,000–2,000 m
Temperate Forests	TF	28,468 km²	1,800–3,000 m
Tropical Eastern Forests	TEF	80,884 km²	200–1,000 m
Tropical Northwestern Forests	TNWF	36,919 km²	0–1,000 m
Tropical Southwestern Forests	TSWF	36,449 km²	0–600 m

Further, the family Phyllostomidae constitutes the most diverse family of bats inhabiting the Neotropics and represents the most extensive radiation in feeding behaviors among the extant mammalian families (Baker et al. 2016; Cirranello et al. 2016). This extraordinary radiation allowed the emergence of different feeding behaviors and diets ranging from fruits, flowers, insects, crustaceans, blood, pollen, nectar, to small vertebrates (including some species of bats) (Gardner 1977) and plays a key role in the dynamics of Neotropical ecosystems. Six trophic categories (*sensu* Patterson et al. 1996; Patterson et al. 2003) are included in the Family Phyllostomidae: High-Flying Frugivore (HFF), Insecti-Carnivore (ICG), Low-Flying Frugivore (LFF), Omnivorous Nectarivore (OMG), Omnivorous Predator (OMP), and Sanguinivore (SAN). Furthermore, the presence and/or absence of certain species in a determined area provides a good estimate regarding the stage of conservation of that ecosystem (Fenton et al. 1992; Medellín et al. 2000; Jones et al. 2009).

Ecuadorian phyllostomid bats are well represented in natural history collections in Ecuador, in other countries worldwide, and in the scientific literature since the 19th century. To date, 111 species in the Phyllostomidae are recognized from Ecuador (modified from Carrera-Estupiñán 2016). In spite of this species richness, geographic distribution patterns for this family in the Northern Andes, which includes Ecuador, remain poorly known. The goal of the present study was to use robust data on geographic and spatial ecological patterns to determine distributional patterns for phyllostomid bats in Ecuador and to test the hypothesis by Albuja et al. (1980) that zoogeographic units define the distribution patterns ascribed to bats. Finally, our intention was to contribute new knowledge on biogeography, conservation, and management.

MATERIALS AND METHODS

Study area.—Ecuador is located in the northwestern region of South America and comprises a continental portion and the Galápagos Archipelago. It has an area of 256,370 km^2 and borders on Colombia to the north and Peru to the south. Continental Ecuador is located between 1º27' N to 5º01' S and 75º15' W to 81º00' W with an elevation gradient ranging from sea level to 6,310 m (Albuja-V 2002).

Ecuador constitutes a transition zone between the Northern (> 2º North) and Central Andes. This transition is marked by the tectonic rupture of Girón-Cuenca, which has been proposed as the northern limit of the Huancabamba depression and the main division between the Northern and Central Andes (Richter et al. 2008). The Ecuadorian Andes contain the narrowest portion of the Andes (~ 150–180 km wide) and dissect the country into two distinct units (Western and Eastern) each with their own biotic and abiotic characteristics (Coltori 2000). The uplift of the Andes Mountains influenced the topography, weather, soil types, watersheds, rivers, and vegetation types found in the country (Cañadas-Cruz 1983; Lenders and Cook 1995; Sierra 1999; Patterson et al. 2012). In terms of geology, Ecuador contains three geomorphological regions: Coast, Amazon, and Andes (Beck et al. 2008) with distinct alluvial and volcanic soil types in all three regions (Dodson and Gentry 1991).

Another relevant feature of Ecuador involves the movement of sea currents along the coast. The cold Humboldt Current coming from the southern hemisphere collides with the southern movement of warm currents coming from the north, causing the climatic effects known as the “El Niño” and “La Niña” (Bendix et al. 2011). The influence of these marine currents is evident in the annual rainfall cycles and the vegetation found in Ecuador. Numerous rivers, lakes, and watersheds also exist in Ecuador. The Río Napo, in eastern Ecuador, has been hypothesized to be the main natural barrier for animal populations occurring on each side of the river (Albuja 1999). All these features have had a strong influence on biodiversity of the bat fauna in Ecuador, resulting in high levels of species richness and endemism in this area.

Zoogeographic units.—Initially, Albuja et al. (1980) proposed eight zoogeographic units (ZU) for Ecuador (Table 1); however, Albuja-V et al. (2012) added the Pacific unit as a 9th ZU. Each ZU was defined by climate, topography, elevation, and vegetation type. However, detailed information about the validity of these ZUs for different groups of vertebrates is not available and has not been examined thoroughly (Albuja-V et al. 2012). Herein, the Galápagos and the Pacific ZUs (Albuja-V et al. 2012) were not included, due to the lack of distributional records for phyllostomid bats from these areas.

Data sources: *Fieldwork*.—Bats were collected during two scientific expeditions to Ecuador. The first (Sowell Expedition 2001) occurred between July and August 2001, whereas the second (Sowell Expedition 2004) took place from June to August 2004 (see Carrera-E 2003; Fonseca et al. 2003; Carrera et al. 2010). Methods associated with the capture and preparation of scientific voucher specimens followed the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and the Texas Tech Animal Care and Use Committee (Permit # 02217-02).

Data sources: Museum records.—Voucher specimens (skins and fluid preserved specimens with their associated skulls) were examined from the following repositories: United States National Museum (USNM); Museo de Zoología at the Pontificia Universidad Católica del Ecuador (QCAZ); Instituto Nacional de Biodiversidad (INABIO, formerly Museo Ecuatoriano de Ciencias Naturales MECN); and Colección Científica del Departamento de Biología, at the Escuela Politécnica Nacional del Ecuador (MEPN).

Data sources: *Scientific literatur*e.—Records of bats collected in Ecuador since the 19th century were obtained from several scientific journals and technical reports including: Thomas (1897); Allen (1916); Anthony (1921, 1923, 1924); Sanborn (1941); Brosset (1965); Linares and Naranjo (1973); Baker (1974); Carter and Dolan (1978); Hill (1980); Albuja (1982, 1999); Webster and Jones (1984); Pacheco and Patterson (1992); Rageot and Albuja (1994); Solmsen (1998); Tirira (1999, 2008, 2009, 2012a, 2012b); Reid et al. (2000); Iudica (2000); Jarrín-V (2001); Fonseca-N and Jarrín-V (2001); Bravo-Cabezas et al. (2003); Hoffmann et al. (2003); Baker et al. (2004); Dávalos (2004); Fonseca and Pinto (2004); Muchhala et al. (2005); Velazco (2005); Hoofer and Baker (2006); Lee et al. (2006a, 2006b, 2008, 2010); McCarthy et al. (2006); Solari and Baker (2006); Pinto et al. (2007); Fonseca et al. (2007); Woodman (2007); Dávalos and Corthals (2008); Gardner (2008); Hoofer et al. (2008); Velazco and Patterson (2008, 2013, 2014, 2019); Solari et al. (2009); Velazco and Gardner (2009); Carrera et al. (2010); Jarrín-V et al. (2010); Larsen et al. (2010); Clare et al. (2011); Jarrín-V and Kunz (2011); Jarrín-V and Menéndez-Guerrero (2011); McDonough et al. (2011); Guerra-M and Albuja-V. (2012); Jarrín-V and Coello (2012); Regalado and Albuja (2012); Tirira and Burneo 2012; Jarrín-V and Clare (2013); Hurtado and Pacheco (2014); Parlos et al. (2014); Tavarez et al. (2014); Bolzan et al. (2015); Calderón-Acevedo and Muchhala (2018); and Velazco et al. (2018). Records of *Sturnira aratathomasi* were not considered in the analyses due to the lack of detailed geographic information from Ecuador (see Peterson and Tamsitt 1968), nor records of *Micronycteris schmidtorum* (Morales-Martínez et al. 2018) because they were published after the statistic and geographic analyses for this study were performed. Further, phyllostomid bats records from Yasuní and Podocarpus National Parks (Rex et al. 2008) were not considered due to the lack of voucher specimens deposited in natural history museums.

Organization of the data.—A total of 13,262 records for phyllostomid bats, representing 109 species with confirmed taxonomic identifications and verified geographic information, were examined (see Appendix I). Detailed information regarding voucher specimens is described in Carrera-Estupiñán (2016). Geographic information for each bat record included was validated using ArcGIS 10.6 (ESRI 2017), Google Earth, and the Convert Geographic Units Website maintained by Montana State University (accessed on 23 April 2019) <http://www.rcn.montana.edu/resources/converter.aspx>. The matrix included in these analyses was based only on bat records with complete taxonomic identification, museum accession number, and verified geographic information (geographic coordinates including degrees, minutes, and seconds; standard UTM; decimal degrees; and elevation in meters).

Taxonomy in this study followed Gardner (2008) unless more recent revisions were available. Exceptions included: Velazco and Patterson (2008) for the recognition of species in the genus *Platyrrhinus*; Larsen et al. (2010) for the recognition of *Artibeus aequatorialis*; Velazco and Simmons (2011) for recognized species in the genus *Vampyrodes*; Jarrín-V and Clare

(2013) and Velazco and Patterson (2013) for taxonomic considerations in the genus *Sturnira*; Hurtado and Pacheco (2014) for the recognition of the new genus *Gardnerycteris*; Parlos et al. (2014) for new arrangements in the subfamily Lonchophyllinae; and Velazco et al. (2018) for the recognition of *Platyrrhinus umbratus*. The use of *Anoura aequatoris* (Mantilla-Meluk and Baker 2006) and *Anoura peruana* (Mantilla-Meluk and Baker 2010) was retained in this study.

Data analysis.—To examine the limits of the zoogeographic units (ZUs) proposed by Albuja et al. (1980) for Ecuador, all phyllostomid records were geo-referenced and assigned into each ZU. Species composition was generated for each ZU and unique species distributed within each ZU were considered to be representative of that ZU. Additionally, to examine the biogeographic affinities of each ZU, a non-metric Multidimensional Scaling analysis (MDS, de Leeuw and Heiser 1982; Stevens et al. 2004) was estimated using a binary Jaccard distance matrix based on species presence/absence. To confirm the strength of these analyses, a Detrended Correspondence Analysis (DCA, Hill and Gauch 1980; Ter Braack 1986) based on relative abundance was performed. This analysis has been used in ecological studies to measure the relationship between taxa and environmental variables (e.g., Owen 1990; Chase et al. 2000; Nakagawa et al. 2006). ZUs were used as the ecological variables and all analyses were performed using PAST 3.06 Software (Hammer et al. 2001).

Species modeling.—Spatial data (geolocations and localities) were filtered based on accuracy (i.e., locality described matched with coordinate location) and standardized to the same datum (WGS84) using ArcGIS 10.6. Species distribution models (SDM) were performed based upon a likelihood analysis for species habitat modeling (Phillips et al. 2006) using maximum entropy niche analysis software (MaxEnt-3.3.3).

Graduated spatial rarefying analyses of the occurrence data via principal component and climate heterogeneity analyses were conducted to eliminate spatial clusters and environmental biases (Boria et al. 2014; Brown 2014; Balaguera-Reina et al. 2019). A total of 24 environmental variables were selected: 19 bioclimatic (bio 1–19, Hijmans et al. 2005), two eco-physiological (mean annual potential evapotranspiration, and mean annual aridity index [Trabucco and Zomer 2009]), a digital elevation model (dem Lehner et al. 2008), and two variables regarding landscape attributes (lctype-landcover type [Broxton et al. 2014a] and mgvf-maximum green variation factor [Broxton et al. 2014b]) at ~1 km^2 resolution (Appendix II). These variables were examined for spatial autocorrelation using the band collection raster tool from ArcGIS 10.6 (Pearson comparison analysis; ESRI 2017), selecting a total of seven variables with $|r| \leq 0.5$ (bio 4, 7, 12, 15, dem, lctype, and mgvf).

Background selection of pseudoabsences was conducted via buffered local adaptive convex-hull analysis (Brown 2014) based upon a 10-km buffer and an alpha value of 3. This combination was selected after testing different values to define the bias file. It is also the most reliable one based on general bat ecology (Fleming and Eby 2003; Cryan and Diehl 2009). These background points also were compared with the rarefy occurrence data to ascertain environmental conditions in which bats can potentially occur, as well as to avoid commission errors and over-fitting the model (Anderson and Raza 2010; Brown 2014).

A geographically structured k-fold cross-validation analysis was performed, dividing the landscape into three regions based on spatial clustering of occurrence points. Five model feature class types (Linear, Quadratic, Hinge, Product, and Threshold) were examined, using 1 as a regularization multiplier to optimize the MaxEnt model performance. From these analyses, the best model was defined based on the omission rates (the lowest value), the area under the curve (AUC, the highest value; Boria et al. 2014), and model feature class complexity (the simplest one; Brown 2014). Finally, a jackknife test of variable importance was performed to define which variables contained the most useful information for the model, as well as which ones contained information not present in the other variables (Brown 2014).

A box-and-whiskers plot was used to define the probability of occurrence threshold based upon the distribution of the dataset via R (R Development Core Team 2012). This only included values above quartile group 1 (minimum) excluding outliers (Balaguera-Reina et al. 2019). Models were added to estimate hotspots (areas with high probability of presence for phyllostomids) and richness across Ecuador throughout zoogeographic units. Shapiro-Wilk tests were performed to determine the normality of the data, and Kruskal-Wallis tests were run to analyze its variability across zoogeographic units. Dunn's-test for independent samples with a Bonferroni adjustment of *P*-values was used to determine pairwise differences of mean ranks when Kruskal-Wallis tests were significant ($P < 0.05$).

Results

Bat diversity among zoogeographic units.—All phyllostomid species listed are included in Appendix I along with their appropriate zoogeographic units (ZU). The Tropical Northwestern Forest included 2,462 records representing 65 species of bats. The most abundant species in this ZU were: *Carollia perspicillata*, *Carollia castanea*, *Artibeus ravus*, *Artibeus rosenbergi, A. aequatorialis*, and *Glossophaga soricina*. *Choeroniscus periosus*, *Diaemus youngi*, *Hsunycteris cadenai*, *L. fornicata*, *M. giovanniae*, *Platyrrhinus vittatus*, and *Vampyriscus nymphaea* are known to occur only in this ZU (McCarthy et al. 2000; Dávalos 2004; Albuja-V and Gardner 2005; Fonseca et al. 2007; Woodman 2007; Lee et al. 2010; Jarrín-V and Kunz 2011; McDonough et al. 2011).

The Tropical Southwestern Forest included 1,182 records for 43 species with *Artibeus fraterculu*s, *A. aequatorialis*, and *G. soricina* being the most abundant species. In Ecuador, *S. bakeri* is endemic to this ZU (Velazco and Patterson 2013).

The Subtropical Western Forests included a total of 1,530 records from 54 species. The most abundant species were *A. fraterculus*, *C. perspicillata*, and *Sturnira ludovici*. *Lonchophylla hesperia* and *Lonchophylla orcesi* are restricted to this ZU (Albuja-V 1991; Albuja-V and Gardner 2005).

The Temperate Forests included 595 records from 21 species with *Anoura geoffroyi* and *Sturnira erythromos* being the most represented species. There were no species restricted to this ZU.

In the High Andes, a total of 193 records representing nine species were retrieved. *Anoura geoffroyi* and *S. erythromos* were the most abundant species. The species *Sturnira bogotensis* and *Sturnira bidens* were found at sampling localities over 3,000 m in the Ecuadorian Andes (Albuja 1982; Pacheco and Patterson 1992; Moreno-Cárdenas 2009; Jarrín-V and Clare 2013). In spite of no phyllostomid species restricted to this unit, it is important to mention that *Mormoops megalophylla* (Mormoopidae) has been recorded only in upper localities from the High Andes of Ecuador (Boada et al. 2003; Camacho et al. 2017).

Eastern Subtropical Forests were represented by a total of 2,179 records from 59 species, and *Carollia brevicauda* was identified as the most abundant species. The species *Vampyressa melissa* and *Glyphonycteris sylvestris* were restricted to this ZU and are known only from three sampling localities in Ecuador (Rageot and Albuja 1994; Tavares et al. 2014; Tirira et al. 2016).

The Tropical Eastern Forests is the most studied, collected, and diverse ZU in Ecuador, with 5,124 bat records and 71 species being recorded. The species *Artibeus lituratus, Artibeus obscurus*, *C. brevicauda*, *C. castanea*, *C. perspicillata*, *Desmodus rotundus*, *Lophostoma silvicolum*, *Phyllostomus elongatus*, *Platyrrhinus infuscus*, *Rhinophylla pumilio*, *Sturnira giannae* (historically *Sturnira lilium,* and *Sturnira* new sp. 3 *sensu* Velazo and Patterson 2013), *Sturnira magna*, *Uroderma bilobatum*, and *Vampyressa thyone* were represented by ≥ 100 records. There were 11 species endemic to the Tropical Eastern Forests: *Glossophaga commissarisi*, *Hsunycteris pattoni*, *Lampronycteris brachyotis*, *Lichonycteris degener*, *Lionycteris spurrelli*, *Lonchophylla orienticollina*, *Lophostoma carrikeri*, *Platyrrhinus angustirostris*, *Platyrhinus incarum*, *Sphaeronycteris toxophyllum*, and *Uroderma magnirostrum* (Baker 1974; Albuja 1982, 1999; Webster and Jones 1984; Albuja-V and Mena-V 1991; Solmsen 1998; Reid et al. 2000; Dávalos and Corthals 2008; Gardner 2008b; Velazco et al. 2010; Lim et al. 2010; McDonough et al. 2010; Tirira et al. 2010; Clare et al. 2011; Tirira 2012; Camacho et al. 2014, 2016).

Although no bats have been recorded from the Galapagos Islands, the geographic modeling depicted this ZU as an area suitable for phyllostomids. However, this model would require migratory or unusual dispersal events for bats to potentially reach/inhabit this region.

Geographic distribution of Ecuadorian phyllostomids across zoogeographic units includes species that are distributed in all the ZUs, and species that have been recorded in a single ZU. There are three species distributed broadly across all the ZUs (*C. perspicillata*, *Enchisthenes hartii*, *Micronycteris megalotis*) and 25 species have been recorded in only one ZU (Appendix I). The numbers of bat species restricted to each ZU are as follows: Tropical Northwestern Forests (*n* = 7), Tropical Eastern Forests (*n* = 11), Subtropical Western Forests (*n* = 2), Subtropical Eastern Forests (*n* = 1), and Tropical Southwestern Forest (*n* = 1). There were no species restricted to the Temperate Forests and High Andes ZUs.

Most recorded species exhibit broad distributions across the Neotropics (Gardner 2008; Reid 2009). However, several species are endemic to large neotropical ecoregions such as the Chocó, Amazonia, or the Andes. For example, *C. periosus* and *Rhinophylla alethina* are restricted to the Tropical Northwestern Forests, but also occur in the Chocó (*sensu* Solari et al. 2012). *Artibeus gnomus*, *Rhinophylla fischerae*, and *U. magnirostrum* are recorded from the Tropical Eastern Forests but also are representative of the broader Amazonian bat fauna. Several bat species, such as *L. orcesi*, *L. fornicata*, *M. giovanniae*, and *S. perla*, are known only from the collecting locality, or have a narrow geographic distribution. Therefore, their potential geographic ranges may be underestimated.

Spatial variation among Zoogeographic Units.—Multidimensional scaling (Fig. 1) and DCA (Fig. 2), depict more similarities in species composition between Pacific (Tropical Northwestern Forest, Tropical Southwestern Forest), Andean (High Andean and Temperate Forests), and Amazonian (Subtropical Eastern Forests and Tropical Eastern Forests) ZUs. Likewise, pairwise comparisons based on the Jaccard Index obtained from a comparison of species composition between ZUs revealed closer similarities between the Pacific, Amazonian, and Andean ZUs (Table 2).

Species modeling.—From the 109 species with geolocations recorded in Ecuador, 51 accurate models for species were generated (average AUC minus standard deviation > 0.5), mainly due to lack of accurate spatial information for the remainder. A total of 5,630 occurrence data points (average number of occurrences per species = 110 ± 116) were collected from reliable sources for all 51 species modeled. Of these, 1,657 geolocations (training samples) were selected after the graduated spatial rarefying analysis was performed (average number of occurrences per species = 32 ± 25 geolocations). An average of 32 ± 24 folds per species model were performed depending on the number of geolocations present. The maximum average area under the curve (AUC) value obtained was 0.975 and the minimum was 0.764. The environmental variable that contributed the most to all models was bio15 [precipitation seasonality; 17 species; percentage of contribution (PC) = 58 ± 13%; permutation importance (PI) = 54 ± 21] followed by the digital elevation model (DEM) (13 species; PC = 67 ± 19%; PI = 68 ± 20), bio12 (annual precipitation; 9 species; PC = 63 ± 16%; PI = 30 ± 28), and bio7 (temperature annual range; 8 species; PC = 62 ± 15%; PI = 51 ± 29).

Based on the results of the jackknife test of variable importance, bio15 (precipitation seasonality) had the highest gain when used in isolation for the majority of species (21) and appears to contain the most useful information, followed by DEM (10 species) and bio 12 and 7 (9 species, respectively). These same environmental variables decreased the gain the most when omitted and thus appear to contain information that is not present in the other variables.

Probability of presence (the chance a species can be found in a defined pixel based on the total pixels analyzed) based upon the rarefied occurrence data indicated that most of the species occurred with a 0.4 probability (40 % chance to be found in a defined pixel) and oscillated around 0.41 ± 0.10 and 0.69 ± 0.08 (upper and lower quartile ± standard deviation; Fig. 3). The minimum lower quartile reported for all species was 0.16 and the maximum upper quartile was 0.86.

Based on the zoogeographic units postulated by Albuja et al. (1980), the Tropical Eastern Forest had the highest probability of presence (13.64 ± 2.52) for the

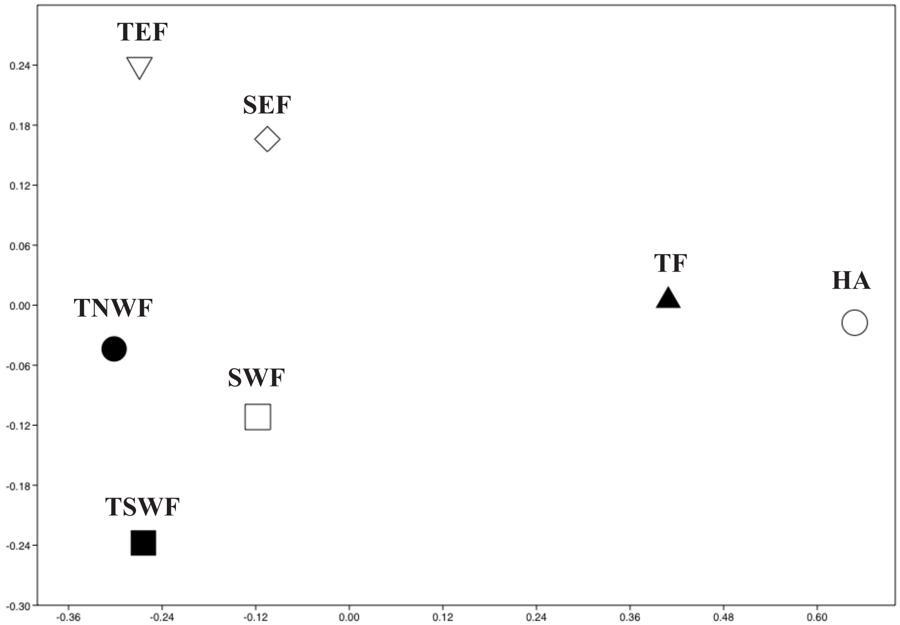

Figure 1. Proximity of seven Zoogeographic Units (ZUs) based on presence/absence of phyllostomid bat species. The graphic depicts first two axes of Non-metric Multidimensional Scaling based on Jaccard Index. ZU acronyms as follows: Tropical Northwestern Forest (TNWF); Tropical Southwestern Forest (TSWF); Subtropical Western Forest (SWF); Temperate Forest (TF); High Andean Forest (HA); Subtropical Eastern Forest (SEF); and Tropical Eastern Forest (TEF).

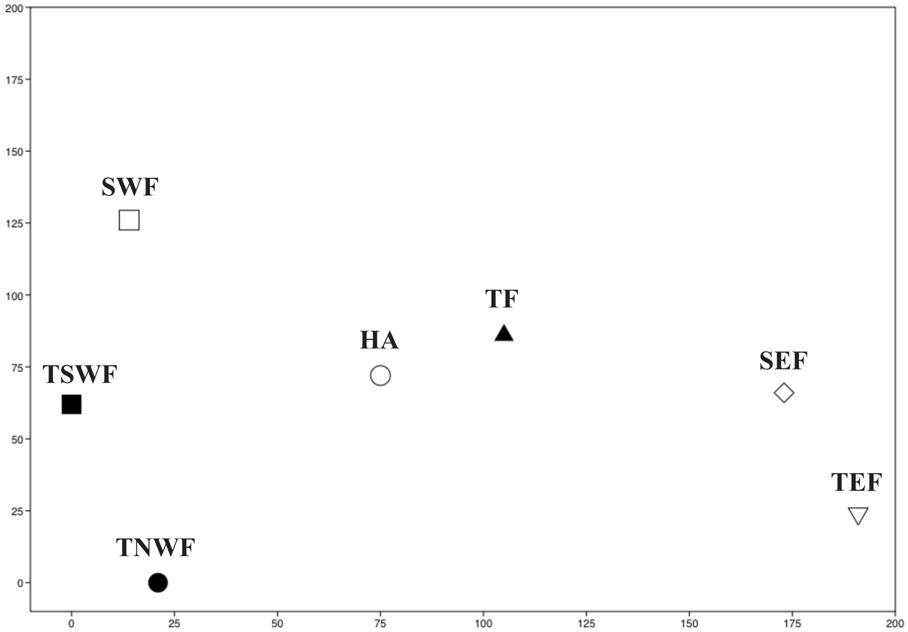

Figure 2. Detrended Canonical Correspondence Analysis (DCA) depicting changes in species composition among Zoogeographic Units (ZUs) defined by Albuja et al. (1980). Graphic is depicting first two DCA axes based on relative abundance of species of Ecuadorian bats. Acronyms of ZUs defined in Figure 1.

Table 2. Pairwise comparisons using the Jaccard index (Real and Vargas 1996) for the seven continental Zoogeographic Units (ZUs) proposed by Albuja et al. (1980). This index, ranging from 0 to 1, compares similarity based on species composition for each ZU. The higher the value, the more similar are the zoogeographic units. ZU acronyms as follows: Tropical Northwestern Forests (TNWF); Tropical Southwestern Forests (TSWF); Subtropical Western Forests (SWF); Temperate Forests (TF); High Andes (HA); Subtropical Eastern Forests (SEF); and Tropical Eastern Forests (TEF).

	TNWF	TSWF	SWF	TF	HA	SEF	TEF
TNWF	1	0.561	0.61	0.225	0.101	0.395	0.432
TSWF	0.561	1	0.65	0.196	0.12	0.371	0.352
SWF	0.61	0.65	1	0.305	0.137	0.444	0.372
TF	0.225	0.196	0.305	1	0.45	0.311	0.21
HA	0.101	0.12	0.137	0.45	1	0.131	0.094
SEF	0.395	0.371	0.444	0.311	0.131	1	0.67
TEF	0.432	0.352	0.372	0.21	0.0945	0.67	1

51 phyllostomid bats modeled, followed by Subtropical Eastern Forest (7.79 ± 2.49), Tropical Northwestern Forest (7.67 ± 2.78), Tropical Southwestern Forest (6.69 ± 2.30), Subtropical Western Forest (6.16 ± 2.37), Temperate Forest (4.62 ± 2.14), and High Andes (2.97 ± 1.55; Fig. 4 left, Fig. 5 left). Concomitantly, the richest zone based on our models is the Tropical Eastern Forest with 19.40 ± 5.47 species, followed by Tropical Northwestern Forest (10.62 ± 4.43 species), Tropical Southwestern Forest (8.74 ± 3.32 species), Subtropical Eastern Forest (8.72 ± 3.36 species), Tropical Southwestern Forest (6.59 ± 2.82 species), Temperate Forest (4.69 ± 2.65 species), and High Andes (3.03 ± 1.77 species; Fig. 4 right, Fig. 5 right).

Probability of presence and richness based on ZUs were significantly different (KW chi-squared = 22911, df = 7, *P*-value < 2.2e-16, and KW chi-squared = 50972, df = 7, *P*-value < 2.2e-16, respectively). The pairwise comparison using Dunn's-test shows that on average the probability of presence and richness across ZUs were significantly different with the exception of TF and TNWF and SEF (Dunn's Test *P* = 1.000).

Six trophic guilds were identified across the 51 species modeled: Sanguinivore (SAN); omnivorous predator (OMP); Omnivorous Nectarivore (OMG); Low-Flying Frugivore (LFF); Insecti-Carnivore (ICG); and High-Flying Frugivore (HFF). However, only four were included (HFF, LFF, ICG, and OMG) due to the limited number of species (≤ 5) in the SAN and OMP guilds (Fig. 6).

HFF and ICG were highly diverse in the Tropical Eastern Forest ZU as well as in the northern part of the Tropical Northwestern Forest and Tropical Southwestern Forest ZUs. ICG and OMG were not present in the High Andes and Temperate Forest but were present in lowland areas as well as LFF. There was a clear spatial pattern across HFF highly correlated with ZUs. Nevertheless, ICG were less correlated with ZUs. In contrast, LFF and OMG were diverse in lowlands without an identifiable pattern across ZUs. However, it is important to highlight that this lack of pattern could be influenced by the limited number of records and species in these two trophic guilds.

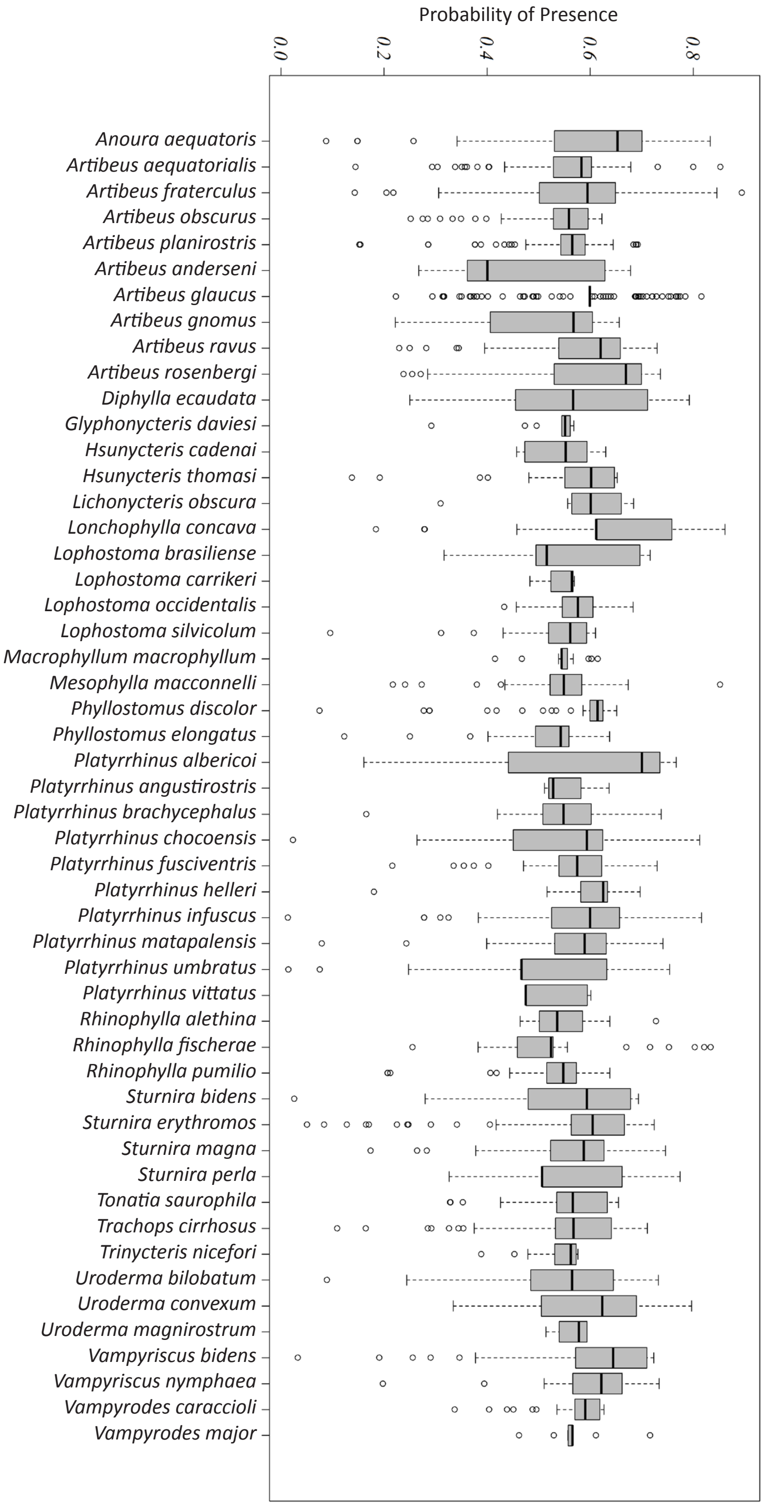

Figure 3. Box and whiskers analysis illustrating the probability of presence for the 51 species of phyllostomids modeled from the relative occurrence rate (ROR). These were based upon the rarefy occurrence data expressed as median and quartiles with whiskers at minimum and maximum values. Outliers are represented as open circles.

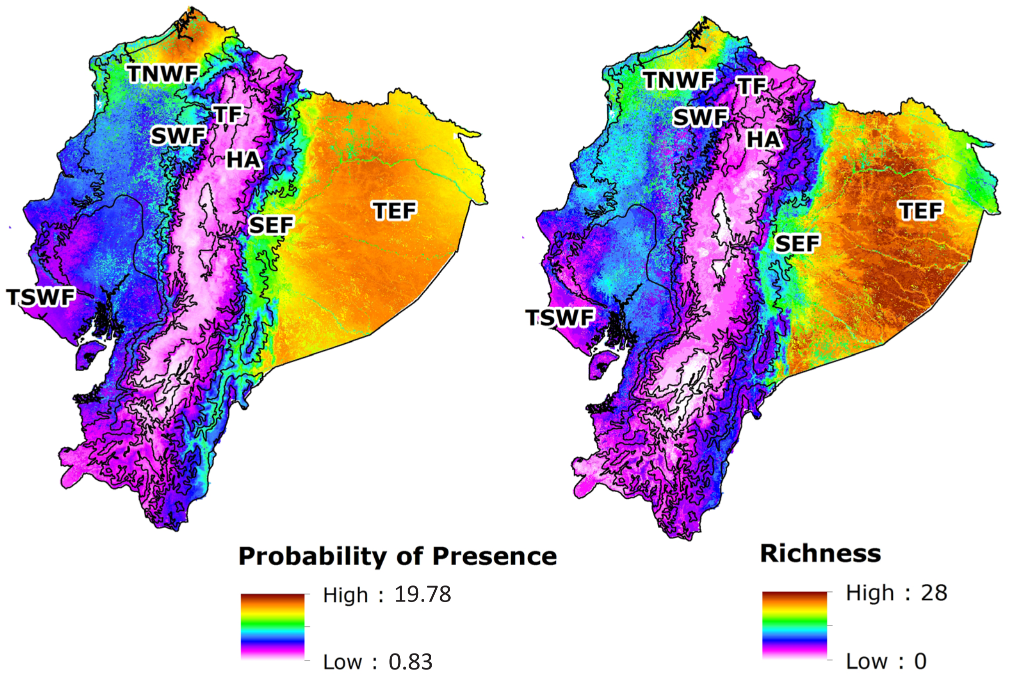

Figure 4. Probability of presence (left) and richness (right) maps based on the 51 phyllostomid bats modeled overlapping the ZUs (black lines and acronyms) defined by Albuja et al. (1980). Warm colors depict areas with high probability of presence, and richness cold colors low presence. Zoogeographic Units (ZUs) acronyms as follows: Tropical Northwestern Forest (TNWF); Tropical Southwestern Forest (TSWF); Subtropical Western Forest (SWF); Temperate Forest (TF); High Andean Forest (HA); Subtropical Eastern Forest (SEF); and Tropical Eastern Forest (TEF).

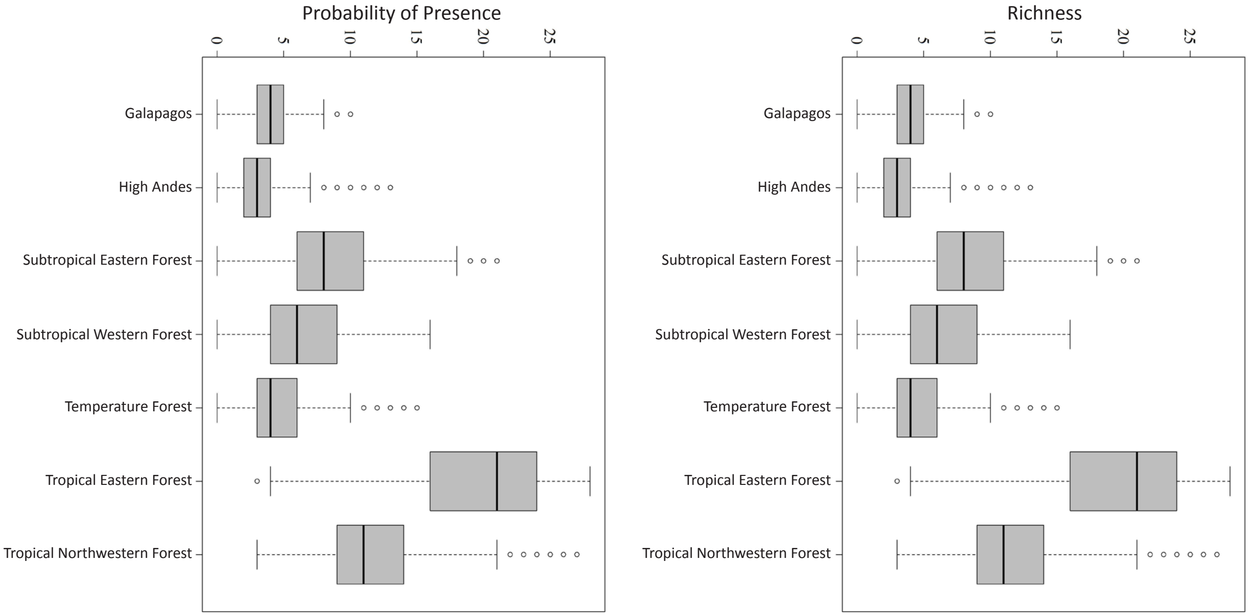

Figure 5. Box and whiskers analysis illustrating the probability of presence (left) and richness (right) for the 51 species of phyllostomids modeled by ZUs described by Albuja et al. (1980). These are expressed as median and quartiles with whiskers at minimum and maximum values. Outliers are represented as open circles.

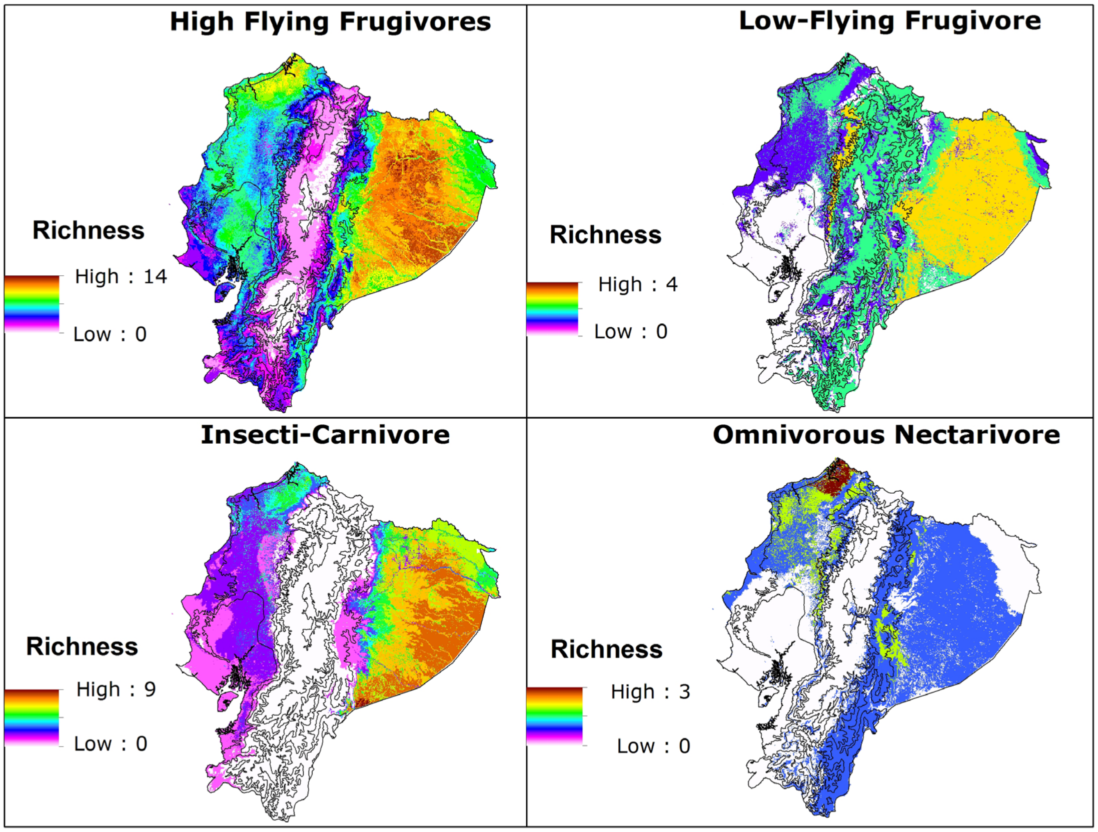

Figure 6. Richness maps based on the 51 phyllostomid bats modeled and classified by trophic guilds overlapping the Zoogeographic Units (ZUs) in black lines defined by Albuja et al. (1980).

Discussion

The diversity of Phyllostomidae bats in Ecuador is a complex mosaic resulting from endemic, rare, common, and broadly distributed species across the Neotropics. Nonetheless, geographic distributions and statistical analyses of phyllostomid bats partially supported the validity of most ZUs proposed within the country. Further, it is possible to recognize differences based on species composition among units.

There are species whose distributions were found to be fully or partially restricted and/or endemic to these ZUs (Appendix I). There are "endemic" species in most of the ZUs with the exception of the Temperate and High Andean forests. However, some species that currently are restricted to a single ZU display broad distribution across the Neotropics. For example: *Vampyriscus nymphaea* recorded in TNWF is distributed broadly from the Pacific side of Ecuador and Colombia to Nicaragua (Arroyo-Cabrales 2008); *D. youngi* currently is known from one sampling locality in TNWF but is broadly distributed in South America, Trinidad and Tobago, and Central America (Kwon and Gardner 2008); *G. commissarisi* is recognized from one locality in Tropical Eastern Forest but recorded in sampling localities from the Amazon basin forest, Central America, and Mexico (Griffiths and Gardner 2008); *S. toxophyllum* is known from two sampling localities in Tropical Eastern Forest (Albuja-V and Mena-V 1991; this study) and currently recorded from Venezuela, Colombia, Peru, Brazil, and Bolivia (Gardner 2008b); *G. sylvestris*, recently reported in the Ecuadorian bat fauna from one sampling locality in Subtropical Eastern Forest (Tirira et al. 2016), is widely distributed from Mexico to Brazil (Williams and Genoways 2008); and *M. schmidtorum*, distributed from Brazil to central Mexico (Williams and Genoways 2008), recently was reported from Ecuador (Morales-Martínez et al. 2018). There were two records of *S. aratathomasi* collected in Ecuador and deposited at the Royal Ontario Museum that unfortunately do not include geographic information (Peterson and Tamsitt 1968). This is a rare species, and records for this taxon are from 1,600 to 1,800 m on the eastern side of the Andes (Tamsitt et al. 1986). The confirmation of a sampling locality for this species in Ecuador is still pending.

In the last decade, several new species in the bat family Phyllostomidae were described based on morphological and/or genetic differences (e.g., *Lonchophylla chocoana*, *L. cadenai*, *L. orcesi*, *L. fornicata*, *L. orienticollina*, *M. giovanniae*, *S. perla*, and *S. bakeri*). In the majority of these descriptions, the new species were reported from a single collecting locality and were based only on a few specimens. This increasing diversity suggests it is necessary to continue surveying these sampling localities and to enforce conservation and management efforts in these ZUs. The rapid increase in recognized species suggests that biodiversity in the tropics is still underestimated for cryptic, poorly known taxa such as bats. Moreover, species limits in some Neotropical genera remain unclear (i.e., *Sturnira* and *Anoura*), suggesting the number of recognized species may increase in the near future. These uncertainties of biodiversity information will have an impact in establishing priorities for conservation and management in Ecuador.

In contrast to ZU endemics as indicators, three species have been recorded in all ZUs in Ecuador: *C. perspicillata*, *E. hartii*, and *M. megalotis.* These species are distributed broadly across the Neotropics (Gardner 2008a). The presence of the common vampire bat (*D. rotundus*) across all ZUs is likely an effect of the availability of food due to deforestation and increase of cattle (Albuja 1999).

The results obtained from the MDS, DCA, and Pairwise comparisons based on Jaccard's Index provide evidence that ZUs proposed by Albuja et al. (1980) are valid for phyllostomid bats, although there are no restricted species in Temperate Forests and the High Andes. ZUs also were supported by the species distribution model and statistical analyses performed based on the probability of presence obtained. Also, it is possible to distinguish closer affinities among bat assemblages occurring in the Pacific ZUs (Tropical Northwestern Forest, Tropical Southwestern Forest, and Southwestern Forest) versus Amazonian ZUs (Tropical Eastern Forest and Subtropical Eastern Forest) and Andean ZUs (High Andes and Temperate Forest). These differences in bat composition can be associated with the particular type of vegetation, climate, and soils present in each ZU. Based on the species distribution model, precipitation and elevation were the two most important variables for the majority of species (31 of 51 species) assessed in the present study.

Although it was not possible to recover models for all 109 species of phyllostomids present in Ecuador, a representative sample of this family (*n* =51) was generated to test the validity of ZUs defined by Albuja et al. (1980). Probability of presence values retrieved from all models showed Ecuador as a highly variable landscape with at least seven homogeneous areas (based on the variables used to model) that were significantly related with the ZUs defined by Albuja et al (1980). The Tropical and Subtropical Eastern Forests were the regions with the most suitable areas for phyllostomid bats (Amazon area) followed by Tropical Northwestern and Southwestern Forests. However, richness analyses showed only the northern part of the Amazon and Choco regions (Tropical Eastern Forest and Tropical Northwestern Forest) as the richest areas. This means that even though southern areas of these regions may be suitable for many of the species present in other ZUs, the current richness values present are lower than expected. Additional research should be done to define whether this lower richness and high suitability is due to a lower sampling effort or to an actual absence of species.

High Flying Frugivore and Insecti-Carnivore were the most common trophic guilds found across phyllostomid bats modeled, with a clear spatial pattern across the former and to a lesser extent with the latter. This pattern is relevant because ZUs may be related not only to species but also associated with the ecological role species play in ecosystems. However, the lack of modeled species in the other four trophic guilds identified for phyllostomids bats in Ecuador limited the analyses and conclusions regarding patterns and ZUs. Thus, more studies should be conducted to test how other trophic guilds are related to ZUs.

The significance in recognizing the validity of these ZUs, based on phyllostomid bat distribution, is important to Ecuador. A formal recognition of these categories might be required to establish research priorities and conservation efforts for chiropterans inside the country. Ecuador currently possesses the highest rate of deforestation in South America (Mosandl et al. 2008). This situation allows the expansion of agricultural lands, the advance of open mining, and the increasing use of natural resources to satisfy human needs. In the case of Temperate Forest and High Andes ZUs, it is imperative to continue research to provide a better estimate of bat diversity and the role of the Andes Mountains as a geographic barrier for dispersal and evolution of this group of mammals. Additionally, determining whether these ZUs are valid for other mammalian orders (such as Rodentia, Soricomorpha, and Didelphimorphia) and other taxonomic groups (such as amphibians, reptiles, and birds) is still pending. Future endeavors studying geographic distributions inside ZUs will contribute as well to the basic knowledge and determination of species as keystones for conservation priorities.

ACKNOWLEDGMENTS

We acknowledge the help and support of the Ministerio del Ambiente del Ecuador for the scientific collecting permit No. 023-ICFAU- DNBAP/MA. We thank A. Brown and J. Sowell for facilitating funding that enabled the Sowell Expeditions 2001 and 2004 to Ecuador. The Latin American Student Field Research award from the American Society of Mammalogists and the René Fonseca Memorial Endowment of the Department of Biological Sciences at Texas Tech University provided financial support. We are grateful to K. Helgen and S. Peurach (United States National Museum), the late R. J. Baker and H. Garner (Natural Science Research Laboratory at Texas Tech University), S. Burneo and A. Camacho (Museo de Zoología QCAZ at the Pontificia Universidad Católica del Ecuador), L. Albuja Viteri and P. Moreno (Escuela Politécnica Nacional del Ecuador), and M. Yánez and J. Brito (Museo Ecuatoriano de Ciencias Naturales - INABIO) for allowing us to visit the collections in their institutions. We thank J. Eger (Royal Ontario Museum) and J. Stuhler (Texas Tech University) for facilitating information included in this study. We especially recognize D. Peñafiel-Zurita for his valuable help in creating the shapefile of the Zoogeographic Units. We thank H. H. Genoways, L. Bradley, and two anonymous reviewers for their valuable comments and suggestions that definitely improved the quality of this paper.

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