On the absence of the Green-tailed Trainbearer
*Lesbia nuna* (Trochilidae) from Venezuela: an analysis based on environmental niche modelling

Paolo Ramoni Perazzi†, Karl L. Schuchmann§†, Magdiel Ablan Bortone¶, Alejandra Soto Werschitz#

† Centro de Simulación y Modelos, Facultad de Ingeniería and Laboratorio de Zoología Aplicada, Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela
§ Zoological Research Museum A. Koenig - ZFMK/Ornithology, Adenauerallee 160, 53113, Bonn, Germany
¶ Universidade Federal de Mato Grosso - UFMT/ Biociencias, Zoologia (Prof. Visitante), Member of the UFMT, Computational Bioacoustics Research Unit - CO.BRA, Cuiaba, Brazil
# Laboratorio de Zoología Aplicada, Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela

Corresponding author: Paolo Ramoni Perazzi (rpaolo1967@gmail.com)

Abstract

Background

*Lesbia nuna*, a hummingbird distributed in the tropical Andes, has been included in Venezuela’s bird list on the basis of a specimen collected in 1873 at Sierra Nevada, Mérida and deposited in the Natural History Museum, London, with no further records for this country since then. This record, largely considered as valid by most authors, has been questioned by others, although without formal analyses.

New information

The potential habitat range of the Green-Tailed Trainbearer, *Lesbia nuna gouldii* (Trochilidae), in the northern Andes from Ecuador to Venezuela was modelled, using
maximum entropy niche modelling, environmental covariates and records from locations across the Colombian Andes. The predicted suitable habitat range corresponded well to the known range of the subspecies *L. n. gouldii* in Colombia and clearly excluded Sierra Nevada. Therefore, these analyses suggest that this species should be removed from the Venezuelan bird list.

**Keywords**

*Lesbia nuna gouldii*, suitable habitat, model, distribution, Colombia, Venezuela

**Introduction**

*Lesbia nuna*, a hummingbird inhabiting the tropical Andes between 1700 and 3800 m (Schuchmann 1999), is currently divided into five (Clements et al. 2016) or seven (Züchner et al. 2017) subspecies, with *L. n. gouldii* being patchily distributed in the central and southern Andes of Colombia. There is also a specimen of this subspecies deposited in the Natural History Museum, London: a male labelled as collected by Anton Goering in 1873 at “Sierra Nevada, Merida, Venezuela”, with no further records made for this country since then (Restall et al. 2006). This record has been largely considered as valid by several authors (Meyer de Schauensee 1964, Meyer de Schauensee and Phelps 1978, Meyer de Schauensee 1982, Hilty and Brown 1986, Fjeldså and Krabbe 1990, Schuchmann 1999, Weller and Schuchmann 2004, Restall et al. 2006, Clements et al. 2016, Züchner et al. 2017), but questioned by Hilty (2003) and excluded by BirdLife International (2017), although without formal analyses.

Habitat alteration often follows the assessment of newly explored areas, with the concomitant extinctions (Fuller 2001). In such cases, species or populations from these areas known only from old single records are usually viewed with scepticism because the lack of further information suggests simply mislabelled specimens (for example Zimmer 1951). Some of these “mysteries” are rediscovered decades or centuries after their scientific descriptions (Scheffers et al. 2011), thus clarifying their situation. Nevertheless, most cases remain obscure, even after intensive and extensive field efforts, because the basic paradox of extinction documentation is that absence of evidence does not mean evidence of absence (Stine and Wagner 2005).

In such cases, ecological niche models (hereafter ENMs; Araújo and Peterson 2012, Peterson et al. 2012, Warren 2012) may constitute fast, convenient and reliable tools, since they can determine the actual distribution of secretive, restricted or rare taxa, information that can otherwise be challenging to obtain because robust empirical field information is often prohibitively expensive. These computer-based mathematical procedures approximate the areas containing a combination of ecological and environmental factors that may underpin the successful performance of a given taxon. ENMs have found extensive application in areas such as biogeography and phylogeography (Alvarado-
Serrano and Knowles 2013, Catullo et al. 2013), or evolutionary biology (Lira-Noriega and Peterson 2014, Silva et al. 2014, Zhang et al. 2014) amongst others, being widely used to extrapolate observed patterns and predict taxa’s geographical distributions using occurrence information data and spatial layers of abiotic conditions (elevation, climate etc.) under past, current or future conditions. For example, Brown et al. (2015) successfully predicted new locality records for the Blue-fronted Lancebill (*Doryfera johannae*) from southeast Peru, ca. 470 km to the southeast of the range reported in literature.

The goal of the present study was to develop ENMs for the *L. n. gouldii* hummingbird subspecies in the northern Andes, from Ecuador to Venezuela, in order to determine whether its range actually reaches the Sierra Nevada in the latter country.

**Materials and methods**

**Study area**

The northern Andes from Ecuador to Venezuela (ca. 4°S to 11°N; sensu Montgomery et al. 2001) are characterised by their SW-NE trending resulting from the collision of the Panamanian arc and the Caribbean Plate against the South America plate (Kennan 2000) and the presence of parallel ridges. In Ecuador, however, the Western and Central Cordilleras are separated by a depression filled by sediments and the product of volcanic eruptions (Coltorti and Ollier 2000), while in Colombia both are separated by the deep intermontane Cauca Valley and the Magdalena valley separates the Central and Eastern Cordilleras. In Venezuela, the Eastern Cordillera splits into the Perijá and Mérida ranges.

In the northern Andes, climate is influenced by the Intertropical Convergence Zone, thus both slopes receive high annual precipitation rates (Jimenez and Oliver 2005) and the concomitant fluvial erosion maintains narrow mountain ranges compared to the remnant chain (Montgomery et al. 2001). In general, precipitation follows the unimodal rainfall pattern typical of Northern South America (Hastenrath 1984) or the typical bimodal pattern towards the Caribbean region (Taylor and Alfaro 2005).

The vegetation is distributed in longitudinal belts along slopes, imperfectly correlated with elevation. Upper slopes, below the snowline, are covered by "páramo", a herbaceous vegetation co-dominated by grasses and *Espeletia* (Compositae), while lower slopes are covered by forests, with a treeline of usually around 3200-3500 m associated with the 6°C isotherm of mean annual temperature (Holdridge 1967, van der Hammen 1974).

During the late Tertiary and the Quaternary, orbital forcing promoted several alternating cold and warm stages with major consequences for biota composition and distribution, especially during the Last Glacial Maximum (hereafter LGM, ca. 20 kyr BP), through mechanisms that are still being debated (Ramírez-Barahona and Eguiarte 2013). During LGM, vegetation belts were located at elevations 1000–1500 m below their current levels (van der Hammen 1974, Bush et al. 1990, Hooghiemstra and der Hammen 2004, Brunschön and Behling 2009, Valencia et al. 2010). This downslope disposition of belt
vegetation types would have promoted the connectivity amongst currently isolated high-
elevation ecological islands.

Today, the biota is also laterally segmented in physiognomically similar but taxonomically
differentiable ecoregions occupying contiguous areas of the slopes (Olson et al. 2001).
Such patterns, originating in the relictuation/expansion process of the ice ages, may be
currently maintained not only by orographic barriers but also by ecological factors, such as
edaphic differences similar to those thought to determine biodiversity patterns in the
Amazon basin (Salo 1987).

García-Moreno and Fjeldså (2000) stated that “vicariant forms are valid species which
remain ecologically incompatible for long periods, possibly because they are subject to
uniform selection pressures”. Thus, considering the lack of evident physical barriers
separating the parapatric taxa *L. n. gouldii* and *L. n. gracilis* as a control to correctly access
the possibility of the occurrence of *L. nuna* in Venezuela, those ENMs that predicted the
minimum area of suitable habitat for *L. n. gouldii* in Ecuador were selected.

**Spatial autocorrelation**

The correction of biases in geographic space is an important step in avoiding models
“overfitting” in environmental space. This is effected by sub-sampling the occurrence
database and reducing the autocorrelation, sacrificing statistical power in favour of
increasing the statistical independence of sampling units (Boria et al. 2014, de Oliveira et
al. 2014, Varela et al. 2014). Therefore, ~10% (four) of the localities were removed from the
dataset, selected through a recursive jackknife process that identified and progressively
removed the localities with the highest contribution to autocorrelation based on Moran's I
coefficients using the “APE” package in R (Paradis et al. 2004, Paradis 2012) and a matrix
of spatial weights (*W*<sub>ij</sub>) calculated as the inverse distance between locations *i* and *j* (1/*d*<sub>ij</sub>)
which was estimated using the Haversine function in the “geosphere” package, version
1.3-13, in R (Hijmans 2015), for all non-categorical environmental variables using the
values measured at the *L. nuna* occurrence points in Colombia.

**Environmental covariates**

The bioclimatic and elevation layers provided by Worldclim, version 1.4 (Hijmans et al.
2005; from [www.worldclim.com](http://www.worldclim.com); 2.5 min resolution) were used. Two categorical covariates
in the modelling process were also evaluated. First, geological provinces, based on
geological data from Schenk et al. 1999, were coded. Second, soil types based on the
Harmonised World Soil Database, version 1.2 (FAO et al. 2012) were coded. Although
land-cover data has been successfully used to obtain more accurate spatial predictions
(Tingley and Herman 2009), this covariate was excluded because the present dataset
included specimens recorded/collected over a long period in a region characterised by high
habitat transformation rates (Food and Agriculture Organization of the United Nations
2010).
The grids of variables used in this study were processed using the libraries “raster” version 2.3-12 (Hijmans 2014), “SDMTools” version 1.1-221 (VanDerWal et al. 2014), “maptools” version 0.8-30 (Bivand and Lewin-Koh 2014) and “rgdal” version 0.9-1 (Bivand et al. 2014), projected to the same coordinate system (EPSG:4248).

To remove the effects of multi-collinearity, Pearson’s correlations between continuous variables, polyserial correlations between continuous and categorical variables and polychoric correlations between the categorical variables for those pixels where *L. nuna* was present, were tested. The highly correlated variables (*r* ≥ 0.75, *p* ≥ 0.001) were excluded from further analysis.

**Distribution predictions**

Four variable combinations were evaluated: continuous variables alone (= climate and elevation; hereafter CON), continuous variables and geology (C+G), continuous variables and soil (C+S), and the combination of all (ALL). There are several ENM algorithms whose performances have been compared by several authors (e.g. Elith et al. 2006, Pearson et al. 2006, Phillips et al. 2006, Terribile et al. 2010, Poor et al. 2012, Merow and Silander 2014). However, only MaxEnt was chosen (version 3.3.3k, from http://biodiversityinformatics.amnh.org/open_source/maxent/, Phillips et al. 2004, Phillips et al. 2006) because the authors were not focused on model comparison since comparative studies demonstrated a similar or better performance for MaxEnt.

To remove the uncertainty that arises from differing use of pseudo-absence points, model predictions were cross-validated, conducting 10 runs, splitting training and test data on a 90:10 ratio and 1000 maximum iterations. As it was assumed that the *L. n. gouldii* occurrence data is biased, a bias grid was built with the same dimensions, cell size and projection as the environmental variables with relative sampling probabilities of 1 for the elevation range from 700 m a.s.l (the alleged lowest elevation range of this hummingbird during LGM) and above and -9999 elsewhere. Projections were made for each run and the average projection, according to the corresponding standard deviation, were created. The significance of each variable was tested through jackknifing.

Binary maps of presence/absence were created to facilitate the visualisation of model predictions. Different threshold methods result in discrepancies in omission errors and unsuitable areas (Nenzén and Araújo 2011, Bean et al. 2012, Liu et al. 2013, Syfert et al. 2013, Norris 2014). Therefore, the results obtained were compared for each of the four variable combinations using seven of the threshold methods available in MaxEnt: Minimum training presence, Fixed cumulative value 1, Fixed cumulative value 5, Fixed cumulative value 10, 10 percentile training presence, Equal training sensitivity and specificity and Maximum training sensitivity plus specificity.

In each case, the mean logistic threshold value was used from the ten runs to determine the amount of false negatives (omissions) and the suitable area predicted for the control country (Ecuador), selecting those having the lower false negatives (omissions) and, at the
same time, predicting the smaller area for the control country to determine the suitable area in Venezuela.

Data resources

Occurrence records

For ENMs, information was gathered on presence localities for *L. nuna* in Colombia which was considered as belonging to *L. n. gouldii* from three main sources. First, information relating to 21 collections from Canada, Colombia, The Netherlands, United Kingdom and United States, whose information is provided online in VertNet ([vertnet.org](http://vertnet.org)), BioMap ([www.biomap.net](http://www.biomap.net)), or gbif.org (2017) or was kindly provided by the respective curator after request was gathered. Second, information from specialised articles on fauna inventories or bird ecology (Willis and Schuchmann 1993, Olivares 1996, Losada-Prado et al. 2005, Echeverry-Galvis and Morales-Rozo 2007, Agudelo-Álvarez et al. 2010, Amaya-Villarreal and Renjifo 2010, Peraza 2011, Andrade-L and Benitez-Castañeda 2012) was obtained. Third, field recordings and videos reported in the specialised databases xeno-canto ([www.xeno-canto.org](http://www.xeno-canto.org)) and the internet bird collection [www.hbw.com/ibc](http://www.hbw.com/ibc) were obtained. Duplicate and redundant localities were removed from the dataset. Records of dubious origin and outliers with respect to the published geographic range were also excluded from the analyses.

The information provided by the citizen-science data was used, i.e. human observations (hereafter Appendix 2, available at [http://cobra.ic.ufmt.br/web/guest/publications-data_sets](http://cobra.ic.ufmt.br/web/guest/publications-data_sets)) from the web-based repositories eBird Basic Dataset (2017), (Sullivan et al. 2009) and gbif.org (2017), were excluded from ENMs but considered as an additional control against which to compare the predictions generated.

The quality of georeferencing of these localities varied from GPS recordings to coordinates of the nearest towns listed on specimen labels. A variety of gazetteers and scientific publications to infer coordinates from the available locality information or to corroborate/correct this information when provided by the source consulted were used.

There is a specimen of *L. nuna* in the American Museum of Natural History (No. 38126) whose locality is simply “Pamplona” and this is probably the reason why authors such as Meyer de Schauensee (1982) included Norte de Santander Department, Colombia, within the range of *L. nuna*. That is outside the remaining collecting localities: a “very uncertain locality” according to BioMap. Therefore, two sets of analyses were undertaken: one including and another excluding such a record. The rationale behind this was (1) to test the validity of this record and (2) to test models including an occurrence as close as possible to the Venezuela border in order to “force” the ENMs to predict suitable areas in that country.
On the absence of the Green-tailed Trainbearer Lesbia nuna (Trochilidae) ...

Taxon treatment

Lesbia nuna

Materials

a. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Campus Pontificia Universidad Javeriana; decimalLatitude: 4.629340; decimalLongitude: -74.064932; associatedReferences: Agudelo-Álvarez et al. (2010); occurrenceID: AgudeloAlvarezETAL201001

b. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Cerros Orientales; decimalLatitude: 4.693056; decimalLongitude: -74.024167; associatedReferences: Peraza (2011); occurrenceID: Peraza201101

c. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Cerros Orientales; decimalLatitude: 4.689722; decimalLongitude: -74.018056; associatedReferences: Peraza (2011); occurrenceID: Peraza201102

d. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Cerros Orientales; decimalLatitude: 4.698889; decimalLongitude: -74.013889; associatedReferences: Peraza (2011); occurrenceID: Peraza201103

e. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Cerros Orientales; decimalLatitude: 4.712778; decimalLongitude: -74.020278; associatedReferences: Peraza (2011); occurrenceID: Peraza201104

f. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-908; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ908

g. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-0934A; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ0934A

h. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-0935A; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ0935A

i. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-0936A; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ0936A

j. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-0936B; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ0936B

k. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.651711; decimalLongitude: -74.061979; catalogNumber: MHNCSJ-0937A; collectionID: Museo de Historia Natural Colegio San José; collectionCode: MHNCSJ; occurrenceID: MHNCSJ0937A

l. scientificName: *Lesbia nuna*; country: Colombia; county: Bogota DC; locality: Chapinero; decimalLatitude: 4.653764; decimalLongitude: -74.064726; catalogNumber: MLS-2405; collectionID: Universidad de la Salle; collectionCode: MLS; occurrenceID: MLS2405
m. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: El Chicó, Bosque; **decimalLatitude**: 4.675878; **decimalLongitude**: -74.054810; **catalogNumber**: ICN-7818; **collectionID**: Instituto de Ciencias Naturales; **collectionCode**: ICN; **occurrenceID**: ICN7818

n. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: La Cita; **decimalLatitude**: 4.750000; **decimalLongitude**: -74.033300; **catalogNumber**: ICN-7823; **collectionID**: Instituto de Ciencias Naturales; **collectionCode**: ICN; **occurrenceID**: ICN7823

o. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: La Floresta, (Usaquén); **decimalLatitude**: 4.700000; **decimalLongitude**: -74.033300; **catalogNumber**: MLS-2408; **collectionID**: Universidad de la Salle; **collectionCode**: MLS; **occurrenceID**: MLS2408

p. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: La Floresta, (Usaquén); **decimalLatitude**: 4.700000; **decimalLongitude**: -74.033300; **catalogNumber**: MLS-2408; **collectionID**: Universidad de la Salle; **collectionCode**: MLS; **occurrenceID**: MLS2408

q. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: San Cristobal Boqueron; **decimalLatitude**: 4.566600; **decimalLongitude**: -74.083300; **catalogNumber**: MHNSJ-0840A; **collectionID**: Museo de Historia Natural Colegio San José; **collectionCode**: MHNSJ; **occurrenceID**: MHNSJ0840A

r. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: San Cristobal Boqueron; **decimalLatitude**: 4.566600; **decimalLongitude**: -74.083300; **catalogNumber**: MHNSJ-839; **collectionID**: Museo de Historia Natural Colegio San José; **collectionCode**: MHNSJ; **occurrenceID**: MHNSJ839

s. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: Usoaquin (and "Usaquen, en la Sabana"); **decimalLatitude**: 4.700000; **decimalLongitude**: -74.033300; **catalogNumber**: MLS-2404; **collectionID**: Universidad de la Salle; **collectionCode**: MLS; **occurrenceID**: MLS2404

t. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: Usoaquin (and "Usaquen, en la Sabana"); **decimalLatitude**: 4.700000; **decimalLongitude**: -74.033300; **catalogNumber**: MLS-2406; **collectionID**: Universidad de la Salle; **collectionCode**: MLS; **occurrenceID**: MLS2406

u. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: Usoaquin (and "Usaquen, en la Sabana"); **decimalLatitude**: 4.700000; **decimalLongitude**: -74.033300; **catalogNumber**: UNIANDES-W/No.; **collectionID**: Universidad de los Andes; **collectionCode**: UNIANDES; **occurrenceID**: UNIANDESNUMBER

v. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: Vivero Venado de Oro; **decimalLatitude**: 4.616990; **decimalLongitude**: -74.064060; **catalogNumber**: IAvH-6138; **collectionID**: Instituto Alexander von Humboldt; **collectionCode**: IAvH; **occurrenceID**: IAvH6138

w. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: [Suba] Humedal Córdoba; **decimalLatitude**: 4.717409; **decimalLongitude**: -74.071884; **associatedReferences**: Andrade & Benitez -Castañeda (2012); **occurrenceID**: AndradeANDBenitezCastañeda201201

x. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: [Suba] Humedal La Conejera; **decimalLatitude**: 4.781048; **decimalLongitude**: -74.065361; **associatedReferences**: Andrade & Benitez -Castañeda (2012); **occurrenceID**: AndradeANDBenitezCastañeda201202

y. **scientificName**: *Lesbia nuna*; **country**: Colombia; **county**: Bogota DC; **locality**: [Torca] Humedal de Torca; **decimalLatitude**: 4.809401; **decimalLongitude**: -74.040813;
On the absence of the Green-tailed Trainbearer Lesbia nuna (Trochilidae) ...

associatedReferences: Andrade & Benítez -Castañeda (2012); occurrenceID: AndradeANDBenitezCastañeda201203

z. scientificName: Lesbia nuna; country: Colombia; county: Bogota DC; locality: El Prado, Sabana de Bogotá, 5 km al norte de Bogotá, Laq. El Prado; decimalLongitude: -74.066600; decimalLatitude: 4.716600; catalogNumber: ICN-7817; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7817

aa. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Chiquinquirá; locality: Chiquinquirá, 10 KM ESE; decimalLongitude: -73.793158; decimalLatitude: 5.557898; catalogNumber: MVZ-120505; collectionID: MVZ; occurrenceID: MVZ120505

ab. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Jenesano; locality: Tibaná; decimalLongitude: -73.383300; decimalLatitude: 5.316600; associatedMedia: Internet Bird Collection (http://ibc.lynxeds.com/photo/green-tailed-trainbearer-lesbia-nuna/male-feeding-blackberry-flower); occurrenceID: InternetBirdCollectionLesbiaNunaMale01

ac. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Miraflores; locality: Miraflores; decimalLongitude: 5.197629; decimalLatitude: -73.198574; catalogNumber: Xeno-Canto-79764; occurrenceID: XenoCanto79764

ad. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Sogamoso; locality: Sogamoso; decimalLongitude: 5.716600; decimalLatitude: -72.933300; catalogNumber: MHN-UCC-W/No.; collectionID: Universidad del Cauca; collectionCode: MHN-UCC; occurrenceID: MHNUCCTONUMBER

ae. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Tunja; locality: Motavita; decimalLongitude: 5.583300; decimalLatitude: -73.383300; associatedReferences: Olivares (1966); occurrenceID: Olivares196601

af. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Cerro Aguablanca; decimalLongitude: 2.246129; decimalLatitude: -76.396385; catalogNumber: USNM - 446180; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446180

ag. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Popayán; decimalLongitude: 2.450000; decimalLatitude: -76.600000; catalogNumber: NHM - 1933.11.14.3; collectionID: Natural History Museum London; collectionCode: NHM; occurrenceID: NHM1933.11.14.3

ah. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Popayán; decimalLongitude: 2.450000; decimalLatitude: -76.600000; catalogNumber: WFVZ - 9344; collectionID: Western Foundation of Vertebrate Zoology; collectionCode: WFVZ; occurrenceID: WFVZ9344

ai. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLongitude: 2.383300; decimalLatitude: -76.450000; associatedReferences: Olivares (1966); occurrenceID: Olivares196602

aj. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLongitude: 2.383300; decimalLatitude: -76.450000; catalogNumber: USNM446179; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446179

ak. scientificName: Lesbia nuna; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLongitude: 2.383300; decimalLatitude: -76.450000; catalogNumber: USNM446181; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446181
al. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: USNM-446182; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446182

am. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: USNM-446183; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446183

an. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: USNM-446184; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446184

ao. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: USNM-446185; collectionID: National Museum of Natural History; collectionCode: USNM; occurrenceID: USNM446185

ap. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: RMNH-8172; collectionID: Nationaal Natuurhistorisch Museum; collectionCode: RMNH; occurrenceID: RMNH8172

aq. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: YPM-026942; collectionID: Yale Peabody Museum; collectionCode: YPM; occurrenceID: YPM026942

ar. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Puracé; decimalLatitude: 2.383300; decimalLongitude: -76.450000; catalogNumber: YPM-026943; collectionID: Yale Peabody Museum; collectionCode: YPM; occurrenceID: YPM026943

as. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Coconuco; decimalLatitude: 2.350000; decimalLongitude: -76.500000; occurrenceRemarks: Excluded from ENMs; associatedReferences: Olivares (1966); occurrenceID: Olivares196603

at. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Coconuco; decimalLatitude: 2.350000; decimalLongitude: -76.500000; catalogNumber: INCIVA-1020; occurrenceRemarks: Excluded from ENMs; collectionID: Instituto Vallecaucano de Investigaciones; collectionCode: INCIVA; occurrenceID: INCIVA1020

au. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Coconuco; decimalLatitude: 2.350000; decimalLongitude: -76.500000; catalogNumber: INCIVA-1021; occurrenceRemarks: Excluded from ENMs; collectionID: Instituto Vallecaucano de Investigaciones; collectionCode: INCIVA; occurrenceID: INCIVA1021

av. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Coconuco; decimalLatitude: 2.350000; decimalLongitude: -76.500000; catalogNumber: INCIVA-1022; occurrenceRemarks: Excluded from ENMs; collectionID: Instituto Vallecaucano de Investigaciones; collectionCode: INCIVA; occurrenceID: INCIVA1022

aw. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Boyaca; municipality: Popayán; locality: Coconuco; decimalLatitude: 2.350000; decimalLongitude: -76.500000; catalogNumber: INCIVA-1023; occurrenceRemarks: Excluded from ENMs; collectionID:
On the absence of the Green-tailed Trainbearer Lesbia nuna (Trochilidae) ...
bi. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Choachí; locality: Choachí; decimalLatitude: 4.533300; decimalLongitude: -73.933300; catalogNumber: ANS-149172; collectionID: Academy of Natural Sciences Philadelphia; collectionCode: ANS; occurrenceID: ANS149172

bj. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Choachí; locality: Choachí; decimalLatitude: 4.533300; decimalLongitude: -73.933300; catalogNumber: ANS-149173; collectionID: Academy of Natural Sciences Philadelphia; collectionCode: ANS; occurrenceID: ANS149173

bk. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Chocontá; locality: Represa del Sisga; decimalLatitude: 5.083300; decimalLongitude: -73.716600; catalogNumber: ICN-7819; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7819

bl. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Chocontá; locality: Represa del Sisga; decimalLatitude: 5.083300; decimalLongitude: -73.716600; catalogNumber: ICN-7820; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7820

bm. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Chocontá; locality: Represa del Sisga; decimalLatitude: 5.083300; decimalLongitude: -73.716600; catalogNumber: ICN-7824; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7824

bn. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Cota; locality: Parque La Florida; decimalLatitude: 4.736399; decimalLongitude: -74.146557; associatedReferences: Andrade & Benitez -Castañeda (2012); occurrenceID: AndradeANDBenitezCastañeda201204

bo. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Gachancipá; locality: Gachancipá; decimalLatitude: 5.000000; decimalLongitude: -73.883300; catalogNumber: ANS-167969; collectionID: Academy of Natural Sciences Philadelphia; collectionCode: ANS; occurrenceID: ANS167969

bp. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Gachancipá; locality: Gachancipá; decimalLatitude: 5.000000; decimalLongitude: -73.883300; catalogNumber: ANS-167979; collectionID: Academy of Natural Sciences Philadelphia; collectionCode: ANS; occurrenceID: ANS167979

bq. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Gachancipá; locality: Gachancipá; decimalLatitude: 5.000000; decimalLongitude: -73.883300; catalogNumber: ICN-7821; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7821

br. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Gachancipá; locality: Gachancipá; decimalLatitude: 5.000000; decimalLongitude: -73.883300; catalogNumber: ICN-7822; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7822

bs. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Gachancipá; locality: Gachancipá; decimalLatitude: 5.000000; decimalLongitude: -73.883300; catalogNumber: MCZ-343415; collectionID: Museum of Comparative Zoology Harvard University; collectionCode: MCZ; occurrenceID: MCZ343415

bt. scientificName: *Lesbia nuna*; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Carretera a Guasca; decimalLatitude: 4.879573; decimalLongitude: -73.883160; catalogNumber: ICN-20152; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN20152
On the absence of the Green-tailed Trainbearer Lesbia nuna (Trochilidae) ...

bu. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Sopó (includes "Valle de Sopó"); decimalLatitude: 4.916600; decimalLongitude: -73.916600; catalogNumber: MLS-2402; collectionID: Universidad de la Salle; collectionCode: MLS; occurrenceID: MLS2402

bv. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Sopó (includes "Valle de Sopó"); decimalLatitude: 4.916600; decimalLongitude: -73.916600; catalogNumber: MLS-2403; collectionID: Universidad de la Salle; collectionCode: MLS; occurrenceID: MLS2403

bw. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Sopó (includes "Valle de Sopó"); decimalLatitude: 4.916600; decimalLongitude: -73.916600; catalogNumber: ICN-7813; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7813

bx. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Sopó (includes "Valle de Sopó"); decimalLatitude: 4.916600; decimalLongitude: -73.916600; catalogNumber: ICN-7814; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN7814

by. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Vda. La Floresta, Fca. La Plata, margen izq. Río Chipatá; decimalLatitude: 4.824200; decimalLongitude: -73.838500; catalogNumber: ICN-33661; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN33661

bz. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guasca; locality: Reserva Biológica el Encenillo; decimalLatitude: 4.841687; decimalLongitude: -73.899978; associatedReferences: Amaya-Villarreal & Renjifo (2010); occurrenceID: Amaya-VillarrealANDRenjifo201001

ca. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Guatavita; locality: Guatavita; decimalLatitude: 4.916600; decimalLongitude: -73.916600; catalogNumber: ICN-33661; collectionID: Instituto de Ciencias Naturales; collectionCode: ICN; occurrenceID: ICN33661

cb. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Pacho; locality: Mountains of Pacho; decimalLatitude: 5.100000; decimalLongitude: -74.166670; associatedReferences: Weller & Schuchmann (2004); occurrenceID: WellerANDSchuchmann200401

cd. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Sibaté; locality: 15 km N Sibate, San Benito Seminario Menor de Bogotá; decimalLatitude: 4.508532; decimalLongitude: -74.260500; catalogNumber: MLS-2400; collectionID: Royal Ontario Museum; collectionCode: ROM; occurrenceID: ROM105389

cc. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Sibaté; locality: Sibaté (includes "Sibate above Bogotá"); decimalLatitude: 4.491300; decimalLongitude: -74.245784; catalogNumber: ICN-7814; collectionID: American Museum of Natural History; collectionCode: AMNH; occurrenceID: AMNH121656

ce. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Sibaté; locality: Sibaté (includes "Sibate above Bogotá"); decimalLatitude: 4.491300; decimalLongitude: -74.260500; catalogNumber: MLS-2400; collectionID: Universidad de la Salle; collectionCode: MLS; occurrenceID: MLS2400

cf. scientificName: Lesbia nuna; country: Colombia; stateProvince: Cundinamarca; municipality: Sibaté; locality: Sibaté (includes "Sibate above Bogotá"); decimalLatitude:
Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Subachoque
locality: La Mar
decimalLatitude: 4.933300
decimalLongitude: -74.183300
catalogNumber: MLS-2397
collectionID: Universidad de la Salle
collectionCode: MLS
occurrenceID: MLS2397

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Subachoque
locality: Subachoque
decimalLatitude: 4.933300
decimalLongitude: -74.183300
catalogNumber: MLS-2398
collectionID: Universidad de la Salle
collectionCode: MLS
occurrenceID: MLS2398

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Subachoque
locality: Subachoque
decimalLatitude: 4.933300
decimalLongitude: -74.183300
catalogNumber: MLS-2399
collectionID: Universidad de la Salle
collectionCode: MLS
occurrenceID: MLS2399

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Susa
locality: Laguna de Fuquene
decimalLatitude: 5.466600
decimalLongitude: -73.750000
catalogNumber: FMNH-220401
collectionID: Field Museum of Natural History
collectionCode: FMNH
occurrenceID: FMNH220401

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Susa
locality: Laguna de Fuquene
decimalLatitude: 5.466600
decimalLongitude: -73.750000
catalogNumber: FMNH-220403
collectionID: Field Museum of Natural History
collectionCode: FMNH
occurrenceID: FMNH220403

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Susa
locality: Laguna de Fuquene
decimalLatitude: 5.466600
decimalLongitude: -73.750000
catalogNumber: FMNH-220404
collectionID: Field Museum of Natural History
collectionCode: FMNH
occurrenceID: FMNH220404

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Susa
locality: Laguna de Fuquene
decimalLatitude: 5.466600
decimalLongitude: -73.750000
catalogNumber: FMNH-220405
collectionID: Field Museum of Natural History
collectionCode: FMNH
occurrenceID: FMNH220405

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Susa
locality: Laguna de Fuquene
decimalLatitude: 5.466600
decimalLongitude: -73.750000
catalogNumber: FMNH-220407
collectionID: Field Museum of Natural History
collectionCode: FMNH
occurrenceID: FMNH220407

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Tabío
locality: Tabío, a orillas del Río Frío
decimalLatitude: 4.916600
decimalLongitude: -74.100000
catalogNumber: ICN-13406
collectionID: Instituto de Ciencias Naturales
collectionCode: ICN
occurrenceID: ICN13406

Lesbia nuna

country: Colombia
stateProvince: Cundinamarca
municipality: Une
locality: Vereda Quimasita [Timasita]
decimalLatitude: 4.425580
decimalLongitude: -74.022600
catalogNumber: ICN-17169
collectionID: Instituto de Ciencias Naturales
collectionCode: ICN
occurrenceID: ICN17169
On the absence of the Green-tailed Trainbearer Lesbia nuna (Trochilidae) ...
Description

Appendix 1. List of localities where *L. nuna* has been recorded in Colombia and included in the modelling process. Coordinates are presented in the decimal degree system. Acronyms: (AMNH) American Museum of Natural History; (ANS) Academy of Natural Sciences, Philadelphia; (DMNH) Delaware Natural History Museum; (FMNH) Field Museum of Natural History; (IAvH) Instituto Alexander von Humboldt; (ICN) Instituto de Ciencias Naturales; (INCIVA) Instituto Vallecaucano de Investigaciones; (IBC) Internet Bird Collection (http://ibc.lynxeds.com/photo/green-tailed-trainbearer-lesbia-nuna/male-feeding-blackberry-flower); (LACM) Natural History Museum of Los Angeles County; (MCBM) Museo Madre Caridad Brader Zahner; (MCZ) Museum of Comparative Zoology, Harvard University; (MHNCSJ) Museo de Historia Natural, Colegio San José; (MHN-UCC) Universidad del Cauca; (MLS) Universidad de la Salle; (MVZ) Museum of Vertebrate Zoology, University of California, Berkeley; (NHM) Natural History Museum, London; (RMNH) Nationaal Natuurhistorisch Museum; (ROM) Royal Ontario Museum; (UNIANDES) Universidad de los Andes; (USNM) National Museum of Natural History; (WFVZ) Western Foundation of Vertebrate Zoology; (XC) Xeno-Canto (www.xeno-canto.org); (YPM) Yale Peabody Museum.
Analysis

Occurrence dataset

The record catalogue number 1888.7.25.185 (Natural History Museum, London) was excluded given its obscure origin (Zimmer 1951). All specimens from “El Guabo” (Nariño) were considered as belonging to the homonymous locality in the Mallama municipality. Information was gathered on 115 records of *L. n. gouldii*, which were reduced to 46 localities after removing duplicates and redundant records and reduced to 42 occurrence data points after removing the ~10% (four) most spatially autocorrelated ones, without counting Pamplona in Norte de Santander Department (Fig. 1). The dataset from the web-based repositories eBird Basic Dataset (2017), (Sullivan et al. 2009) and gbif.org (2017) consisted of 699 sightings (Appendix 2).

Environmental variables

A correlation matrix (Table 1) indicated three groups of highly correlated variables. The first two were integrated by temperature-based variables: (1) Bio01, Bio05, Bio06, Bio08, Bio09, Bio10 and Bio11, which were, in turn, highly correlated with elevation and (2) the pair Bio02 and Bio07. The third group was a set of the precipitation-based variables Bio12, Bio13,
Bio14, Bio16, Bio 17 and Bio 19. Although Bio12 (annual precipitation) and Bio14 (precipitation in the driest month) belonged to the same group, they were not highly correlated with each other, so both were retained for further analyses, in addition to elevation and Bio07 (annual temperature range). Correlations of variables Bio03 (isothermality), Bio04 (temperature seasonality), Bio15 (precipitation seasonality), Bio18 (precipitation in the warmest quarter), soil and geology were below 0.75 in all cases and thus included in the modelling process.

Table 1.

Pearson's correlations between continuous environmental variables, polyserial correlations between continuous and categorical environmental variables and polychoric correlations between the categorical environmental variables for the record localities of Lesbia nuna in Colombia. Continuous variables: Elev, elevation; Bio01, annual mean temperature; Bio02, mean monthly temperature range; Bio03, isothermality; Bio04, temperature seasonality; Bio05, max temperature of the warmest month; Bio06, min temperature of the coldest month; Bio07, temperature annual range; Bio08, mean temperature of the wettest quarter; Bio09, mean temperature of the driest quarter; Bio10, mean temperature of the warmest quarter; Bio11, mean temperature of the coldest quarter; Bio12, annual precipitation; Bio13, precipitation of the wettest month; Bio14, precipitation of the driest month; Bio15, precipitation seasonality; Bio16, precipitation of the wettest quarter; Bio17, precipitation of the driest quarter; Bio18, precipitation of warmest quarter; Bio19, precipitation of the coldest quarter. Categorical variables: Soil and Geol, geology.

|        | Bio01 | Bio02 | Bio03 | Bio04 | Bio05 | Bio06 | Bio07 | Bio08 | Bio09 | Bio10 | Bio11 | Bio12 | Bio13 | Bio14 | Bio15 | Bio16 | Bio17 | Bio18 | Bio19 | Soil | Geol |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|------|
| Elev   | -0.99 | -0.41 | -0.29 | -0.07 | -0.96 | -0.97 | -0.10 | -0.98 | -0.99 | -0.98 | -0.99 | -0.34 | -0.44 | 0.07  | -0.47 | -0.44 | 0.04  | -0.54 | -0.28 | -0.18|
| Bio01  | -      | 0.40  | 0.22  | 0.14  | 0.98  | 0.97  | 0.14  | 1.00  | 1.00  | 1.00  | 1.00  | 0.26  | 0.36  | -0.17 | 0.52  | 0.37  | -0.15 | -0.09 | 0.48  | 0.20  | 0.12 |
| Bio02  | -      | -0.23 | 0.03  | 0.54  | 0.21  | 0.83  | 0.42  | 0.40  | 0.40  | 0.41  | -0.19 | -0.04 | -0.27 | 0.35  | -0.36 | -0.30 | -0.55 | 0.03  | -0.20 | 0.16 |
| Bio03  | -      | -0.44 | 0.09  | 0.40  | -0.74 | 0.20  | 0.22  | 0.18  | 0.24  | 0.61  | 0.54  | 0.58  | -0.12 | 0.54  | 0.59  | 0.60  | 0.27  | 0.58  | 0.62 |
| Bio04  | -      | 0.22  | 0.11  | 0.27  | 0.12  | 0.18  | 0.20  | 0.08  | -0.01 | 0.04  | -0.18 | 0.24  | 0.06  | -0.20 | -0.25 | 0.20  | -0.22 | -0.40 |
| Bio05  | -      | 0.92  | 0.31  | 0.98  | 0.98  | 0.98  | 0.98  | 0.20  | 0.33  | -0.24 | 0.57  | 0.33  | -0.22 | -0.22 | 0.47  | 0.11  | 0.07  |
| Bio06  | -      | -0.10 | 0.96  | 0.97  | 0.96  | 0.96  | 0.42  | 0.50  | -0.02 | 0.47  | 0.50  | 0.01  | 0.07  | 0.56  | 0.31  | 0.17  |
| Bio07  | -      | 0.16  | 0.13  | 0.16  | 0.14  | -0.50 | -0.36 | 0.29  | -0.37 | -0.56 | -0.72 | -0.16 | -0.48 | -0.24 |
| Bio08  | -      | 0.99  | 0.99  | 1.00  | 0.22  | 0.32  | -0.19 | 0.49  | 0.32  | -0.17 | -0.10 | 0.44  | 0.18  | 0.11  |
| Bio09  | -      | 1.00  | 0.99  | 0.29  | 0.39  | -0.14 | 0.51  | 0.40  | -0.12 | -0.09 | 0.52  | 0.21  | 0.11  |
| Bio10  | -      | 0.99  | 0.24  | 0.35  | -0.20 | 0.54  | 0.35  | -0.18 | -0.11 | 0.47  | 0.17  | 0.09  |
| Bio11  | -      | 0.25  | 0.35  | -0.17 | 0.52  | 0.36  | -0.15 | -0.09 | 0.46  | 0.20  | 0.14  |
| Bio12  | -      | 0.95  | 0.72  | -0.09 | 0.97  | 0.77  | 0.61  | 0.86  | 0.56  | 0.23  |
| Bio13  | -      | 0.58  | 0.16  | 0.99  | 0.63  | 0.63  | 0.42  | 0.89  | 0.49  | 0.23  |
| Bio14  | -      | -0.60 | 0.57  | 0.96  | 0.67  | 0.44  | 0.43  | 0.17  |
| Bio15  | -      | 0.12  | -0.58 | -0.49 | 0.12  | -0.19 | 0.05  |
| Bio16  | -      | 0.62  | 0.44  | 0.91  | 0.53  | 0.24  |
| Bio17  | -      | 0.73  | 0.49  | 0.44  | 0.16  |
| Bio18  | -      | 0.26  | 0.34  | 0.09  |
| Bio19  | -      | 0.45  | 0.02  |
| Soil   | -      | 0.46  |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
All variables showed some degree of spatial autocorrelation. Moran’s I coefficients ranged from 0.533 (Bio03) to 0.086 (elevation), averaging 0.290. After removing four localities, these values were substantially reduced to a range between 0.465 (Bio03) and 0.002 (elevation), averaging 0.207. The omission rate on test samples was higher than the predicted omission rate when incorporating soil information. A similar pattern is observed when comparing the areas under the curves amongst the different combination of variables (Fig. 2): the \( \text{AUC}_{\text{Train}} \) is statistically higher than \( \text{AUC}_{\text{Test}} \) when incorporating soil in the analyses. For instance, removing localities and incorporating soil information reduced the influence of the spatial autocorrelation on the models, improving the independence between test and training data.

![Figure 2](image)

**Figure 2.** Comparison of the areas under the curves for both training (black) and test (grey) of the ENMs using the 42 localities where *Lesbia nuna* has been recorded in Colombia (excluding “Pamplona” and the four most highly autocorrelated localities) for each of the four environmental variable combinations: continuous variables alone (= climate and elevation, CON), continuous variables and geology (C+G), continuous variables and soil (C+S) and the combination of all (ALL). “W” and “p” are, respectively, the values of the statistics and the probability of Wilcoxon rank sum tests.

Summary statistics for variables used for ENMs are shown in Table 2. Bioclimatic variables based on temperature showed similar patterns at recording points in Colombia when compared with locations within the same elevational range in the Venezuelan Andes. In contrast, variables involving precipitation showed substantial differences between both areas.
Table 2.
Summary statistics for explanatory variables used in ENMs for the 42 localities where *Lesbia nuna* has been recorded in Colombia and for the same elevational range in the Venezuelan Andes. In the categorical variables, “n” refers to the number of localities (Colombia) or the number of pixels (Venezuela). In Geology, codes correspond to those provided by layer GEO6EXP_ID.

| Variable | Colombia | | | Venezuela | | |
|----------|----------|----------|----------|----------|----------|----------|
|          | Median   | Min      | Max      | Median   | Min      | Max      |
| Elev     | 2614.0   | 1654.0   | 3522.0   | 2263.0   | 1654.0   | 3522.0   |
| Bio03    | 81.0     | 75.0     | 91.0     | 81.0     | 75.0     | 84.0     |
| Bio04    | 303.5    | 185.0    | 640.0    | 428.0    | 339.0    | 608.0    |
| Bio07    | 113.0    | 98.0     | 141.0    | 137.0    | 110.0    | 149.0    |
| Bio12    | 991.5    | 772.0    | 2285.0   | 1021.0   | 706.0    | 1478.0   |
| Bio14    | 35.0     | 20.0     | 123.0    | 22.0     | 8.0      | 38.0     |
| Bio15    | 40.0     | 25.0     | 60.0     | 49.0     | 37.0     | 68.0     |
| Bio18    | 290.5    | 153.0    | 685.0    | 310.0    | 198.0    | 503.0    |
| Nominal  |          |          |          |          |          |          |
| Soil     | 16039    | 17       | 40.5     | 27614    | 172      | 30.8     |
|          | 16047    | 10       | 23.8     | 27615    | 172      | 30.8     |
|          | 16017    | 4        | 9.5      | 27616    | 107      | 19.1     |
|          | 16015    | 4        | 9.5      | 27621    | 59       | 10.6     |
|          | 7        |          | 16.7     |          | Others (04) | 49 | 8.8  |
|          | Others (04) | 7 | 16.7 | Others (04) | 49 | 8.8  |
| Geology  | 219      | 15       | 35.7     | 0        | 138      | 24.7     |
|          | 434      | 6        | 14.3     | 230      | 115      | 20.6     |
|          | 542      | 5        | 11.9     | 219      | 36       | 6.4      |
|          | Others (10) | 19 | 38.1 | Others (33) | 270 | 48.3 |

Occurrence points in Colombia are found in four of the geologic provinces (sensu Schenk et al. 1999): (1) West-Central Cordillera, (2) Cauca Basin, (3) Eastern Cordillera and (4) Llanos Basin. In particular, 35.7% of occurrence points fall in areas of Cretaceous origin, 31.0% during the Tertiary, 11.9% during the Quaternary and 21.4% during other periods. In contrast, the whole area within the elevational range of *L. nuna* belongs to just one of those provinces, the Perijá-Venezuelan Coastal Ranges, where 24.7% of records fall in areas originating in the Precambrian undifferentiated, 20.6% in Paleozoic metamorphics, 6.4% in Cretaceous and 48.3% in other periods.

In Colombia, soils were mostly Leptosols (40.5% of the points), followed by Acrisols (23.8%), various Cambisols (21.4%), various Phaeozems (11.9%) and Luvisols (2.4%) while, in Venezuela, various Cambisols predominated (61.7%), followed by Leptosols (19.0%), Luvisols (10.6%), Ferralsols (5.5%), Solonetz (2.5%) and Arenosols (0.5%)i.e.,
weakly developed soils whose development has been limited by landscape instability (Beek and Bramao 1969, de Castro Portes et al. 2016).

The relative contribution of each environmental variable to the different models is shown in Table 3. Elevation had the highest contribution in the CON model and the corresponding permutation importance (i.e. the jackknife significance test) indicates heavy dependence of this model on that variable. Geology had the highest contribution in the case of the C+G model, but the corresponding permutation importance indicates that this model depends more on elevation. Finally, soil had the highest contribution in the case of the C+S and ALL models.

| Variables | ALL C% | ALL PI | CON C% | CON PI | C+G C% | C+G PI | C+S C% | C+S PI |
|-----------|--------|--------|--------|--------|--------|--------|--------|--------|
| Bio03     | 0.6    | 2.5    | 15.5   | 13.5   | 3.1    | 4.7    | 1.0    | 1.1    |
| Bio04     | 0.2    | 1.3    | 11.3   | 14.5   | 2.2    | 12.0   | 0.5    | 2.3    |
| Bio07     | 0.1    | 0.0    | 0.5    | 0.8    | 0.7    | 1.3    | 0.2    | 0.1    |
| Bio12     | 3.2    | 3.3    | 9.3    | 1.7    | 4.4    | 0.8    | 2.6    | 8.2    |
| Bio14     | 2.1    | 4.1    | 9.5    | 2.9    | 5.0    | 4.5    | 2.4    | 0.5    |
| Bio15     | 1.6    | 3.2    | 5.3    | 8.3    | 1.8    | 6.0    | 1.8    | 1.5    |
| Bio18     | 1.6    | 7.6    | 4.4    | 11.5   | 1.6    | 10.2   | 2.4    | 13.0   |
| Elevation | 19.6   | 22.1   | 44.2   | 46.8   | 29.4   | 37.0   | 20.9   | 27.9   |
| Geology   | 14.1   | 9.3    | -      | -      | 51.8   | 23.5   | -      | -      |
| Soil      | 57     | 46.5   | -      | -      | -      | -      | 68.1   | 45.3   |

**Threshold selection**

All combinations of variables, especially CONs, predicted suitable areas in Ecuador, false negatives in Colombia and suitable areas in Venezuela, when using given thresholds. Two combinations of variables and thresholds performed differentially better (Fig. 3): ALL + Equal training sensitivity and specificity logistic threshold and C+S + Maximum training sensitivity plus specificity logistic threshold.

These combinations only predicted three false negatives in the case of Colombia (Fig. 4) where the suitable habitat for this hummingbird subspecies consists of a relatively wide area on the Cundiboyacense altiplano and smaller to scattered areas in both the Massif of Huaca and along the Central Cordillera up to central Antioquia. These combinations did not
predict suitable areas in Norte de Santander which excludes Pamplona but predicted small suitable areas in Ecuador of 17 or 29 (out of a total of 34) pixels in two small patches at Tungurahua and Loja. These combinations also predicted very small suitable areas for *L. n. gouldii* in Venezuela: 4 and 18 (out of a total of 19) pixels located in eastern-central Táchira and a couple in the westernmost portion of Mérida State i.e. these models did not predict the “Sierra Nevada” as a suitable habitat.

Similar results were achieved when including Pamplona in the ENMs with three main differences: (1) only one combination performed differentially better (*C+S + X10 percentile training presence logistic threshold*), (2) fewer, small and scattered patches of suitable areas predicted in Norte de Santander and (3) the same, but smaller, two patches of suitable areas predicted for Ecuador. This model also predicted some suitable areas for Venezuela similar to, but smaller than those described in the previous paragraph, excluding again “Sierra Nevada, Merida”.

Figure 3. Number of *Lesbia nuna* test localities omitted in Colombia, contrasted against the number of pixels predicted for Ecuador. ● ALL models, ▲ C+S, ○ CON, □ C+G, combined with seven thresholds. A5 refers to ALL model + Equal training sensitivity and specificity logistic threshold and D6 refers to C+S + Maximum training sensitivity plus specificity logistic threshold.
Discussion

Model selection

Habitat suitability for *L. n. gouldii* under current conditions was predicted using bioclimatic variables, elevation, information on geology and soil, as well as data available on the distribution of this hummingbird. However, the highest omission rate on test samples compared to the predicted omission rate and the statistically significant differences between the AUC\textsubscript{Train} and AUC\textsubscript{Test} strongly indicated that models including soil information should be preferred in this case. Moreover, the combination of few omissions of test localities in Colombia and the small area predicted for Ecuador, highlight the convenience of applying the Equal training sensitivity and specificity logistic threshold, as well as the Maximum training sensitivity plus specificity logistic thresholds. The authors' conclusions are based on these modelling conditions.

These predictions fitted almost exactly to the range reported by the independent datasets consulted (Fig. 4), reinforcing the premise that this model consistently retrieves the actual distribution range of *L. n. gouldii* in the northern Andes. This included areas as far as the northernmost portion of the Central Cordillera in Colombia whose validity is corroborated...
by the visual record from Entrerrios (CORANTIOQUIA, catalogue number 4743-5615). In contrast to Meyer de Schauensee (1982), these predictions clearly excluded the whole Norte de Santander Department. Of course, "accidentals" have been largely recognised in literature (e.g. Grinnell 1922), but stable populations are more likely to be absent from Norte de Santander as reinforced by the lack of further records from eBird (Sullivan et al. 2009, eBird Basic Dataset 2017) and gbif.org (2017).

**Contribution of variables**

Climate variability characterised the Holocene (11,500 BP to the present), with several periods of significant rapid climate change of polar cooling, tropical variation of moisture and major atmospheric circulation changes (Mayewski et al. 2004, Polissar et al. 2013). For example, temperature lowered to $-3.2 \pm 1.4^\circ$C and precipitation increased ca. 20% between 1250 and 1810 CE in the Venezuelan Andes, promoting four glacial advances (Polissar et al. 2006) with corresponding changes in the biota. For example, Rull et al. (1987) and Rull and Schubert (1989) postulate that the Little Ice Age caused the lowering of vegetation belts in the Venezuelan Andes during the 15-16th centuries. To succeed in dealing with such environmental uncertainty, organisms would have to follow certain strategies, such as: (1) a conservative bet-hedging that minimises their fitness variance across all possible environmental conditions (Starrfelt and Kokko 2012), (2) a diversification bet-hedging that takes advantage of alternative environmental scenarios in a probabilistic fashion (Starrfelt and Kokko 2012) and (3) an adaptive tracking in which the environmental variation results in correlated variation in mean population traits as natural selection favours different phenotypes over evolutionary time (Cleland et al. 2007). That is, the characteristic climatic unpredictability of most of the “life span” of *L. n. gouldii* may have kept or promoted a plasticity with respect to the tolerance of climatic conditions, as suggested by its wide elevational range and the low to zero contribution of the bioclimatic variables to ALL and C+S models.

Conversely, soil and geology are more stable features and were the most important in *L. n. gouldii* than any other variable when included in the modelling processes. Bedrock geochemistry (Hahm et al. 2014) and soil properties (Aragão et al. 2009, Honorio Coronado et al. 2009, Unger et al. 2012, Muenchow et al. 2013, Arellano et al. 2014) influence plant species distribution, composition, productivity and structure which, in turn, influence animal species abundance and composition (Jankowski et al. 2012, Pomara et al. 2012) and ultimately animal distribution (Peres 2008, Beja et al. 2010), including very mobile ones such as bats (Ramos Pereira et al. 2009).

In South American lowlands, where the effect of physical barriers is expected to be low, a broad range of evidence from plants (Kreft et al. 2004), arthropods (Sigrist and de Carvalho 2009), amphibians (Symula et al. 2003), reptiles (Vanzolini 1988, Sigrist and de Carvalho 2009), birds (Haffer 1987, Prum 1988, Bates et al. 1998) and mammals (da Silva and Oren 1996, Patton and da Silva 1998) indicates an unevenly distributed biodiversity with areas holding high endemism and unique biotas, whose origins, history and ecological mechanisms are debated (Tuomisto and Ruokolainen 1997, Bush 2005, Haffer 2008) but
are consistent with the hypothesis that current patterns of biotic distribution in the Amazon basin are based on edaphic differences (Salo 1987).

Moreover, most of the articles cited in the previous paragraph and (up to a point) one of the currently accepted ecoregional divisions of South America (Olson et al. 2001), point to the Putumayo River as the southernmost limit, similar to that reported by Ramoni-Perazzi et al. (2012) for the mid-elevation-ranging phyllostomid bat Artibeus amplus. Thus, these results suggest the presence of edaphic differences acting as ecological barriers to L. n. gouldii as a possible bottom-up effect of soil properties on the distribution of this hummingbird.

Adaptation to local environmental conditions is a primary driver for morphological evolution and speciation (Schluter 2000, Schluter 2001, Levin 2003). This important stage in the speciation process is identifiable through examination of the ecological niches, thus strengthening support for species delimitation (Funk et al. 2006, Kozak and Wiens 2006, Rissler et al. 2007, Kozak et al. 2008, Wielstra et al. 2012). In the Andes, speciation has been promoted by abundant orographic barriers and step elevational gradients (Vuilleumier 1969, Vuilleumier 1984, Simpson Vuilleumier 1971, Fjeldså 1992) as well as temporary isolation by glacial cycles (e.g. Vuilleumier and Simberloff 1980, Fjeldså 1992, Heindl and Schuchmann 1998, García-Moreno and Fjeldså 2000). In the case of L. n. gouldii, this probably resulted from a population isolated in suitable areas of the Cauca and Magdalena valleys during the LGM evolving in isolation and migrating upslope to suitable areas during the temperature rise in the Holocene. In this context and reinforced by the lack of evident physical barriers separating L. n. gouldii from its neighbour L. n. gracilis, these results are in favour of the proposal of Weller and Schuchmann (2004) to split L. gouldii from L. nuna. Lesbia nuna gouldii in Venezuela

The lack of further L. n. gouldii records for Venezuela can be analysed through three postulates. First, trochilids include long-distance and elevational migrants, acknowledged for their ability to travel long distances. Furthermore, most Andean hummingbird species have patchy distribution patterns including prominent cases such as Eriocnemis luciani, whose population in Ecuador and the extreme southwestern Colombia is separated by a gap of ca. 1100 km in Eastern Cordillera from a population in the Venezuelan Andes (Schuchmann et al. 2001). For instance, L. nuna could have reached the Mérida Cordillera during the LGM and then gone locally extinct simply by chance as shown for insular species on oceanic islands (MacArthur and Wilson 1967, Brown 1978). In fact, Venezuelan Andes are smaller than their Colombian counterparts, hence the lower number of avian species observed in the former. Mapping the elevation of the northern Andes from 700 m a.s.l. (the lowest elevation expected for L. nuna during the LGM) and upwards, shows a continuous belt from Colombia to Venezuela which is interrupted nowadays only by the Táchira depression (Fig. 1) whose efficacy as a biogeographic barrier varies from one taxonomic group to another (Gutiérrez et al. 2015). Therefore, L. n. gouldii should range up to at least the Tama Massif, but this area was excluded by the authors' ENMs and is not supported by collecting/recording information.
Second, *L. n. gouldii* could have occurred in the Venezuelan Andes until historical times but the dynamics of habitat transformation on both sides of the Colombian-Venezuelan border led to its extinction in the latter country. However, similar considerations should be made in this case as in the previous paragraph. Moreover, (1) the “Venezuelan” locality is a well-preserved area minimally impacted by human activities and (2) in Colombia, this hummingbird has been considered “fairly common” (Restall et al. 2006) and some eBird Basic Dataset (2017) records have been made in parks in Bogotá city, highlighting the tolerance of this species to habitat transformation.

Third, this hummingbird was never established in the Venezuelan Andes, as indicated by these analyses. Available data indicate a substantial variation in precipitation and temperature patterns with latitude along the tropical Andes since the LGM and thus regions sharing synchronous changes during one period could be asynchronous during another Bush et al. (2011). For example, from ca. 8000 BP to the present, the climate of northern South America has been influenced by both El Niño-Southern Oscillation and the Intertropical Convergence Zone, but during the Younger Dryas and the early Holocene, western and eastern regions were differentially influenced by these climatic phenomena (Muñoz et al. 2017). In fact, in their GIS-based vegetation map of the world at the time of the LGM, Ray and Adams (2001) indicated differences between the drier Venezuelan Andes, occupied by semi-desert to the northwest and grasslands to the southeast and the wetter Colombian Andes, occupied by a complex topographic mosaic of forests, grasslands and montane deserts. Thus, despite its being very likely that the dispersal capabilities of these hummingbirds could have led them to spread to the Venezuelan Andes at some point in past times, differences in the evolution of environmental conditions could have prevented them establishing there permanently.

Moreover, the information in Fig. 4 strongly suggests that the northeastern limit of *L. n. gouldii* coincides with the Chicamocha Canyon. The origins of the Eastern Cordillera have been debated (Taboada et al. 2000) but widely recognised as resulting from an asynchronous and spatially heterogeneous process, as evidenced by the four “Massifs”: Garzón, Quetame, Floresta and Santander (Restrepo and Toussaint 1988, Case et al. 1991, Restrepo-Pace et al. 1997). From a geological point of view, Mérida and the Eastern Cordilleras are separated by the NW–SE trending Santander Massif and the southern termination of the left-lateral strike-slip Santa Marta-Bucaramanga fault (Audemard M 2003), the system to which the Chicamocha Canyon belongs. From a biogeographical point of view, the Chicamocha Canyon represents a barrier or a discontinuity for several taxa (Cuatrecasas 1979, Cuervo 2013). For example, the frog genus *Rheobates* (Aromobatidae) has a highly supported genetic discontinuity corresponding roughly to a split centred on the Chicamocha Canyon (Muñoz-Ortiz et al. 2014). Amongst birds, within the Long-tailed Antbird species complex, *Drymophila caudata* (Thamnophilidae), characterised by its large range in both latitude (from northern Venezuela to Bolivia) and elevation (800 to 3150 m), the Chicamocha Canyon is the barrier between *D. caudata*, distributed to the southwest and its vicariant *D. klagesi*, found in the northeast (Isler et al. 2012). In addition, the subspecies of the Pale-bellied Tapaculo, *Scytalopus griseicollis* (Rhinocryptidae), ranging between 2000 and 3900 m, are separated from each other by the
system of the Chicamocha Canyon and the Horta-Opón valley (Avendaño and Donegan 2015).

The possibility of an "accidental" status of the "Venezuelan" specimen is also possible, but a clue in this respect can be obtained directly from the alleged collector: Christian Anton Goering. According to Sclater and Salvin (1868), this German ornithologist, painter and explorer, arrived at Carúpano dock, Sucre, on 30th November 1866 and stayed in Venezuela until 1874 (Sclater and Salvin 1875). He was commissioned by the Zoological Society of London to collect specimens of the Venezuelan fauna for the British Museum, arriving in “Merida by way of the Lake of Maracaibo and Zuliar on 5th April, 1869” and “Leaving Merida on 30th of October, 1869, Mr. Goering set out to return by land to Puerto Cabello, intending to collect en route. But reaching Carache, a revolution broke out, which rendered it necessary for him to retreat to the Lake of Maracaibo and so by sea to La Guayra” (Sclater and Salvin 1870). According to Sclater and Salvin (1875), who indicated no precise date but “Previously to his return to Europe last year”, Herr Goering performed a second trip to Mérida when he ascended the Sierra Nevada to (at least) “an altitude of 10,000 feet”, when he would have collected the “Venezuelan” specimen of L. nuna. Then, “After leaving Merida, on his last journey, Mr. Goering traversed the line of the Andes to San Cristoval, in the Province of Tachira, on the frontiers of Columbia” (Sclater and Salvin 1875) without indicating how Herr Goering returned to Caracas.

However, the journey depicted in the previous paragraph contrasts with many of the details narrated by Herr Goering himself in his book published in Leipzig in 1893, translated into Spanish by M. L. de Blay and published by Universidad de Los Andes, Mérida, Venezuela, in 1958, this being the version consulted by the authors. According to Goering (1958), he performed only one journey to the Venezuelan Andes (not two as indicated in the previous paragraph), when besides exploring the surroundings of Mérida city, he performed three round-trip expeditions: (1) towards Torondoy, southern part of the Lake of Maracaibo Basin, crossing the páramo of Sierra de La Culata at Mucuchíes; (2) towards Cúcuta, in Norte de Santander Department, Colombia, crossing the Mocotíes valley and the Táchira State; and (3) towards Sierra Nevada in his attempt to climb “El Picácho de la Colúna” (= “Pico La Columna”, or “Pico Bolívar” since 1925) in June. Then Goering left Mérida intending, as indicated by Sclater and Salvin (1870), to return by land to Puerto Cabello but a revolution forced him to retreat to the Lake of Maracaibo, where he lost part of the specimens collected and then he continued by sea to Puerto Cabello (not Caracas) where he sent the surviving specimens to England. Thereafter, Goering (1958) spent the remaining time in Venezuela surveying Valencia, the Llanos, Guacara and Caracas, where he witnessed three days of fighting in 1870 and where he associated with local and foreign personalities, such as Mr. James Mudie Spence, who promoted an artistic exhibition about the middle of 1872 and where Goering showed some 50 drawings and paintings, some of which were used by Spence (1878). So, according to Goering himself, he was not in Sierra Nevada in 1873, when the “Venezuelan” specimen of L. nuna would have been collected.

Moreover, the book of Goering (1958) contains many remarks on birds collected by him, because of their beauty, as they represented some novelty, as they were new to him etc. With regards to his surveys around Mérida city, he wrote “Characteristic hummingbird
species of these upper forests are *Heliangelus* Spenci, Bourciera Conradi […] and the Sword-bill Hummingbird (Docimastes ensifer)”. In the case of his ascent to Sierra Nevada, an enterprise narrated in an entire chapter of his book, Herr Goering offered a short list of the birds collected: “*Anthus bogotensis, Phrygillus unicolor, Serpophaga cyanea, Ochtoëca superciliosa, Turdus gigas, […] Querquedula andium […]. At an elevation of 3500 m, I found a new species of parrot, the *Conurus rhodocephalus* along with a black and white Water Thrush (*Cinclus leuconotus*). In the shrub area also occurs *Stegnolaema Montagnii*.”

Therefore, it is striking that a spectacular species like *L. nuna* (Fig. 5), whose beauty should have added a note of colour (because “The local fauna found here [at Sierra Nevada] is well adapted [morphologically] to the landscape; no colorful birds nor insects can be observed”) and which would have been new to Herr Goering, representing a new record for Venezuela and an interesting record of this species, was excluded from his report.

All this suggests that the “Venezuelan” specimen was simply a case of mislabelling, “perhaps from the large collections of these birds [hummingbirds] that are constantly being forwarded from the vicinity of Bogotá” (Sclater and Salvin 1870).

In conclusion, it is very unlikely that the range of *L. nuna* extended to Venezuela or that it even occurred in the country as an accidental visitor. In consequence, this species should be removed from the Venezuelan bird list.
Acknowledgements

We are grateful to Mark Adams for providing us with photos of the “Venezuelan” specimen, relevant literature and information on the specimens deposited at The Natural History Museum (NHM), London, UK. We thank the following individuals and institutions for providing data on the specimens used in this study: Paul R Sweet, American Museum of Natural History (AMNH); Claudia Medina and Claudia Munera Roldan, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH); José Joaquín Celeita Bernal, Museo De La Salle Bogota (MLS); Janet Hinshaw, Museum of Zoology of the University of Michigan (UMMZ); Kimball L. Garrett, Natural History Museum of Los Angeles County (NHM); Steven van der Mijl, Naturalis Biodiversity Center (RMNH); Helen James and Christopher Milensky, Smithsonian Institution (NMHN); René Corado, Western Foundation of Vertebrate Zoology (WFVZ). Luis Fernando Chaves and Carlos Rengifo provided us with valuable literature. Miguel Lentino and an anonymous reviewer provided valuable comments on our manuscript. The authors thank Dr. Luis Mazariegos, Cali, Colombia, for the photos of Lesbia nuna he provided. The authors declare that they have no conflict of interests.

Author contributions

All authors included made substantial contributions to conception and design, acquisition of data and/or analysis and interpretation of data: PRP conceived the study; PRP and IASW collected and depurated the occurrence data set; PRP and MAB developed and analysed the ENMs models; PRP and KLS analysed the ENMs outputs from a biological point of view. All four authors participated in drafting the article and revising it critically for important intellectual content and all four authors gave final approval of the version submitted.

References

- Agudelo-Álvarez L, Moreno-Velasquez J, Ocampo-Peñuela N (2010) Colisiones de aves contra ventaneras en un campus universitario de Bogota, Colombia. Ornitología Colombiana 10: 3-10. [In Spanish].
- Alvarado-Serrano D, Knowles LL (2013) Ecological niche models in phylogeographic studies: applications, advances and precautions. Molecular Ecology Resources 14 (2): 233-248. https://doi.org/10.1111/1755-0998.12184
- Amaya-Villarreal AM, Renjifo LM (2010) Efecto del retamo espinoso (Ulex europaeus) sobre las aves de borde en un bosque altoandino. Ornitología Colombiana 10: 11-25. [In Spanish].
- Andrade-L ME, Benitez-Castañeda H (2012) Los Humedales de la Sabana de Bogotá: Área Importante para la Conservación de las Aves de Colombia y el Mundo. http://unicesar.ambientalex.info/infoCT/Humsabbogareimpconavecolmunco.pdf. Accessed on: 2012-7-18.
• Aragão LE, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jiménez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, Anderson LO, Alvarez E, Baker TR, Gonçalvez PH, Huamán-Ovalle J, Mamani-Solórzano M, Meir P, Monteagudo A, Patiño S, Peñuela MC, Prieto A, Quesada CA, Rozas-Dávila A, Rudas A, Silva Jr. JA, Vásquez R (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences 6 (12): 2759-2778. https://doi.org/10.5194/bg-6-2759-2009

• Araújo M, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93 (7): 1527-1539. https://doi.org/10.1890/11-1930.1

• Arellano G, Cala V, Macía M (2014) Niche breadth of oligarchic species in Amazonian and Andean rain forests. Journal of Vegetation Science 25 (6): 1355-1366. https://doi.org/10.1111/jvs.12180

• Audemard M FA (2003) Geomorphic and geologic evidence of ongoing uplift and deformation in the Mérida Andes, Venezuela. Quaternary International 101-102: 43-65. https://doi.org/10.1016/s1040-6182(02)00128-3

• Avendaño J, Donegan T (2015) A distinctive new subspecies of Scytalopus griseicollis (Aves, Passeriformes, Rhinocryptidae) from the northern Eastern Cordillera of Colombia and Venezuela. ZooKeys 506: 137-153. https://doi.org/10.3897/zookeys.506.9553

• Bates J, Hackett S, Cracraft J (1998) Area-relationships in the Neotropical lowlands: an hypothesis based on raw distributions of Passerine birds. Journal of Biogeography 25 (4): 783-793. https://doi.org/10.1046/j.1365-2699.1998.2540783.x

• Bean W, Stafford R, Brashares J (2012) The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography 35 (3): 250-258. https://doi.org/10.1111/j.1600-0587.2011.06545.x

• Beek KJ, Bramao DL (1969) Nature and Geography of South American Soils. In: Fittkau EJ, Illies J, Klinge H, Schwabe GH, Sioli H (Eds) Biogeography and Ecology in South America. 2. Springer, The Hague, 497 pp. https://doi.org/10.1007/978-94-011-9731-1_4

• Beja P, Santos CD, Santana J, Pereira MJ, Marques JT, Queiroz HL, Palmeirim J (2010) Seasonal patterns of spatial variation in understory bird assemblages across a mosaic of flooded and unflooded Amazonian forests. Biodiversity and Conservation 19 (1): 129-152. https://doi.org/10.1007/s10531-009-9711-6

• BirdLife International (2017) Species factsheet: Lesbia nuna . http://www.birdlife.org. Accessed on: 2017-5-16.

• Bivand R, Lewin-Koh N (2014) maptools: Tools for reading and handling spatial objects. R package version 0.8-30. The Comprehensive R Archive Network. Release date: 2014-5-06. URL: https://CRAN.R-project.org/package=maptools

• Bivand R, Keitt T, Rowlingson B (2014) rgdal: Bindings for the geospatial data abstraction library. 0.9-1. The Comprehensive R Archive Network. Release date: 2014-9-18. URL: https://CRAN.R-project.org/package=rgdal

• Boria R, Olson L, Goodman S, Anderson R (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling 275: 73-77. https://doi.org/10.1016/j.ecolmodel.2013.12.012

• Brown AGE, Whitworth AW, Fowler A, Brent-Smith M, Burdekin O (2015) Dorytera johannae (Bourcier, 1847) (Aves: Apodiformes: Trochilidae): new locality, range extension and notes on distribution. Check List 11 (5): 1749. https://doi.org/10.15560/11.5.1749
• Brown JH (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs 2: 209-227. URL: http://www.jstor.org/stable/23376568
• Brunschön C, Behling H (2009) Late Quaternary vegetation, fire and climate history reconstructed from two cores at Cerro Toledo, Podocarpus National Park, southeastern Ecuadorian Andes. Quaternary Research 72 (3): 388-399. https://doi.org/10.1016/j.yqres.2009.07.001
• Bush M (2005) Of orogeny, precipitation, precession and parrots. Journal of Biogeography 32 (8): 1301-1302. https://doi.org/10.1111/j.1365-2699.2005.01343.x
• Bush M, Colinvaux P, Wiemann M, Piper M, K (1990) Late Pleistocene temperature depressions and vegetation change in Ecuadorian Amazonia. Quaternary Research 34 (03): 330-345. https://doi.org/10.1016/0033-5894(90)90045-m
• Bush MB, Hanselman JA, Hooghiemstra H (2011) Andean montane forests and climate change. In: Bush M, Flenley J, Gosling W (Eds) Tropical Rainforest Responses to Climatic Change. Springer-Verlag, Berlin, 454 pp. https://doi.org/10.1007/978-3-642-05383-2_2
• Case JE, Shagam R, Giegengack R (1991) Geology of the northern Andes; An overview. In: Dengo G, Case JE (Eds) The Caribbean Region. H. Geological Society of America, Inc., Boulder. https://doi.org/10.1130/dnag-gna-h.177
• Catullo R, Lanfear R, Doughty P, Keogh JS (2013) The biogeographical boundaries of northern Australia: evidence from ecological niche models and a multi-locus phylogeny of *Uperoleia* toadlets (Anura: Myobatrachidae). Journal of Biogeography 41 (4): 659-672. https://doi.org/10.1111/jbi.12230
• Cleland E, Chuine I, Menzel A, Mooney H, Schwartz M (2007) Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22 (7): 357-365. https://doi.org/10.1016/j.tree.2007.04.003
• Clements JF, Schulenberg TS, Iliff MJ, Roberson D, Fredericks TA, Sullivan BL, Wood CL (2016) The eBird/Clements checklist of birds of the World: v2016. http://www.birds.cornell.edu/clementschecklist/download/. Accessed on: 2017-4-22.
• Coltorti M, Ollier CD (2000) Geomorphic and tectonic evolution of the Ecuadorian Andes. Geomorphology 32: 1-19. https://doi.org/10.1016/s0169-555x(99)00036-7
• Cuatrecasas J (1979) Comparación fitogeográfica de páramos entre varias Cordilleras. In: Salgado-Labouriau ML (Ed.) El medio ambiente páramo. Ediciones Centro de Estudios Avanzados, Mérida, 243 pp. [In Spanish].
• Cuervo AM (2013) Evolutionary assembly of the Neotropical montane avifauna. Louisiana State University, Baton Rouge, 125 pp. URL: http://digitalcommons.lsu.edu/gradschool_dissertations/27
• da Silva JMC, Oren DC (1996) Application of parsimony analysis of endemivity in Amazonian biogeography: an example with primates. Biological Journal of the Linnean Society 59 (4): 427-437. https://doi.org/10.1111/j.1095-8312.1996.tb01475.x
• de Castro Portes R, Spinola DN, Reis JS, Ker JC, da Costa LM, Fernandes Filho EI, Kühn P, Reynaud Schaefer CEG (2016) Pedogenesis across a climatic gradient in tropical high mountains, Cordillera Blanca — Peruvian Andes. CATENA 147: 441-452. https://doi.org/10.1016/j.catena.2016.07.027
• de Oliveira G, Rangel TF, Lima-Ribeiro MS, Terribile LC, Felizola Diniz-Filho JA (2014) Evaluating, partitioning, and mapping the spatial autocorrelation component in
ecological niche modeling: a new approach based on environmentally equidistant records. Ecography 37 (7): 637-647. https://doi.org/10.1111/j.1600-0587.2013.00564.x

- eBird Basic Dataset (2017) Version: EBD_relMay-2017. Ithaca. Cornell Lab of Ornithology. Release date: 2017-5-01.
- Echeverry-Galvis MA, Morales-Rozo A (2007) Lista anotada de algunas especies de la vereda Cerca de Piedra, Chía, Colombia. Colombia Boletin Sae 17 (2): 87-93. [In Spanish].
- Elith J, Graham C, Anderson R, Dudík M, Ferrier S, Guisan A, Hijmans R, Huetttmann F, Leathwick J, Lehmann A, Li J, Lohmann L, Loiselle B, Manion G, Moritz C, Nakamura M, Nakazawa Y, M. Overton J, Peterson AT, Phillips S, Richardson K, Scachetti-Pereira R, Schapire R, Soberón J, Williams S, Wisz M, Zimmermann N (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2): 129-151. https://doi.org/10.1111/j.2006.0906-7590.04596.x
- FAO, IIASA, ISRIC, ISSCAS, JRC (2012) Harmonized World Soil Database. 1.2. Food and Agriculture Organization of the United Nations. Release date: 2012-3-07. URL: http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/HWSD_Data.html?sb=4
- Fjeldså J (1992) Biogeographic patterns and evolution of the avifauna of relict high altitude woodlands of the Andes. Steenstrupia 18: 9-62.
- Fjeldså J, Krabbe N (1990) Birds of the High Andes: a manual to the birds of the temperate zone of the Andes and Patagonia, South America. University of Copenhagen, Copenhagen, 880 pp. [ISBN 87-88757-16-1]
- Food and Agriculture Organization of the United Nations (2010) Global forest resources assessment 2010: Main report. Food and Agriculture Organization of the United Nations, Rome, 372 pp.
- Fuller E (2001) Extinct birds. 1st. Cornell University Press, Cornell, 400 pp. [ISBN 080143954X]
- Funk DJ, Nosil P, Etges WJ (2006) Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. Proceedings of the National Academy of Sciences 103 (9): 3209-3213. https://doi.org/10.1073/pnas.0508653103
- García-Moreno J, Fjeldså J (2000) Chronology and mode of speciation in the Andean avifauna. Bonner Zoological Monographs 46: 25-46.
- gbif.org (2017) GBIF Occurrence Download. The Global Biodiversity Information Facility https://doi.org/10.15468/DL_IURPKG
- Goering A (1958) De las tierras bajas tropicales a las nieves perpetuas. [From tropical lowlands to perpetual snows]. Universidad de Los Andes, Mérida, 172 pp. [In Spanish].
- Grinnell J (1922) The role of the "accidental". The Auk 39: 373-380. https://doi.org/10.2307/23073434
- Gutiérrez E, Maldonado J, Radosavljevic A, Molinari J, Patterson B, Martínez-C. J, Rutter A, Hawkins MR, Garcia F, Helgen K (2015) The taxonomic status of Mazama bricenii and the significance of the Táchira depression for mammalian endemism in the Cordillera de Mérida, Venezuela. PLoS ONE 10 (6): e0129113. https://doi.org/10.1371/journal.pone.0129113
- Haffer J (1987) Biogeography of Neotropical birds. In: Prance GT (Ed.) Biogeography and Quaternary history in tropical America. Clarendon Press, Oxford, 104-150 pp. [ISBN 0198545460].
• Haffer J (2008) Hypotheses to explain the origin of species in Amazonia. Brazilian Journal of Biology 68: 917-947. https://doi.org/10.1590/s1519-69842008000500003
• Hahm WJ, Riebe C, Lukens C, Araki S (2014) Bedrock composition regulates mountain ecosystems and landscape evolution. Proceedings of the National Academy of Sciences 111 (9): 3338-3343. https://doi.org/10.1073/pnas.1315667111
• Hastenrath S (1984) Interannual variability and annual cycle: mechanisms of circulation and climate in the tropical Atlantic sector. Monthly Weather Review 112: 1097-1107.
• Heindl M, Schuchmann K (1998) Biogeography, geographical variation and taxonomy of the Andean hummingbird genus Metallura Gould, 1847. Journal für Ornithologie 139 (4): 425-473. https://doi.org/10.1007/bf01653470
• Hijmans JR (2014) raster: Geographic data analysis and modeling. 2.3-12. The Comprehensive R Archive Network. Release date: 2014-10-18. URL: http://cran.r-project.org/package=raster
• Hijmans RJ (2015) geosphere: Spherical trigonometry. 1.3-13. The Comprehensive R Archive Network. Release date: 2015-4-11. URL: https://CRAN.R-project.org/package=geosphere
• Hijmans RJ, Cameron S, Parra J, Jones P, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25 (15): 1965-1978. https://doi.org/10.1002/joc.1276
• Hilty SL (2003) Birds of Venezuela. 2nd. Princeton University Press, Princeton, 776 pp. [ISBN 9780691092508]
• Hilty SL, Brown WL (1986) A guide to the birds of Colombia. Princeton University Press, Princeton, 996 pp. [ISBN 069108372X]
• Holdridge LR (1967) Life Zone Ecology. Rev. ed. Tropical Science Center, San Jos, 206 pp.
• Honorio Coronado EN, Baker TR, Phillips OL, Pitman NCA, Pennington RT, Martínez RV, Monteagudo A, Mogollón H, Cardozo ND, Ríos M, García-Villacorta R, Valderrama E, Ahuite M, Huamantupa I, Neill DA, Laurance WF, Nascimento HEM, de Almeida SS, Killeen TJ, Arroyo L, Núñez P, Alvarado LF (2009) Integrating regional and continental scale comparisons of tree composition in Amazonian terra firme forests. Biogeosciences Discussions 6 (1): 1421-1451. https://doi.org/10.5194/bgd-6-1421-2009
• Hooghiemstra H, der Hammen TV (2004) Quaternary Ice-Age dynamics in the Colombian Andes: developing an understanding of our legacy. Philosophical Transactions of the Royal Society B: Biological Sciences 359 (1442): 173-181. https://doi.org/10.1098/rstb.2003.1420
• Isler MI, Cuervo AM, Bravo GA, Brumfield RT (2012) An integrative approach to species-level systematics reveals the depth of diversification in an Andean thanamphophilid, the long-tailed Antbird. The Condor 114: 571-583. https://doi.org/10.1525/cond.2012.120012
• Jankowski J, Merkord C, Ríos WF, Cabrera KG, Revilla NS, Silman M (2012) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. Journal of Biogeography 40 (5): 950-962. https://doi.org/10.1111/jbi.12041
• Jimenez N, Oliver JE (2005) South America, Climate of. In: Oliver JE (Ed.) Encyclopedia of World Climatology. Springer Netherlands, Dordrecht, 854 pp. [ISBN 978-1-4020-4870-8].
• Kennan L (2000) Large-scale geomorphology in the central Andes of Peru and Bolivia: Relation to tectonic, magmatic and climatic processes. In: Summerfield MA (Ed.) Geomorphology and Global Tectonics. Wiley, Londo, 396 pp. [ISBN 978-0-471-97193-1].
• Kozak K, Wiens J (2006) Does niche conservatism promote speciation? A case study in North American salamanders. Evolution 60 (12): 2604–2621. https://doi.org/10.1554/06-334.1
• Kozak K, Graham C, Wiens J (2008) Integrating GIS-based environmental data into evolutionary biology. Trends in Ecology & Evolution 23 (3): 141-148. https://doi.org/10.1016/j.tree.2008.02.001
• Kreft H, Köster N, Küper W, Nieder J, Barthlott W (2004) Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. Journal of Biogeography 31 (9): 1463-1476. https://doi.org/10.1046/j.1365-2699.2004.01083.x
• Levin D (2003) The ecological transition in speciation. New Phytologist 161 (1): 91-96. https://doi.org/10.1046/j.1469-8137.2003.00921.x
• Lira-Noriega A, Peterson AT (2014) Range-wide ecological niche comparisons of parasite, hosts and dispersers in a vector-borne plant parasite system. Journal of Biogeography 41 (9): 1664-1673. https://doi.org/10.1111/jbi.12302
• Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40 (4): 778-789. https://doi.org/10.1111/jbi.12058
• Losada-Prado S, Carvajal-Lozano AM, Molina-Martínez YG (2005) Listado de especies de aves de la cuenca del río Coello (Tolima, Colombia). Biota Colombiana 6: 101-115. [In Spanish].
• MacArthur RH, Wilson EO (1967) The theory of island biogeography. 1st. Princeton University Press, Princeton, 203 pp. [ISBN 0691088365]
• Mayewski P, Rohling E, Stager JC, Karlén W, Maasch K, Meeker LD, Meyerson E, Gasse F, Kreveld Sv, Holmgren K, Lee-Thorp J, Rosqvist G, Rack F, Staubwasser M, Schneider R, Steig E (2004) Holocene Climate Variability. Quaternary Research 62 (03): 243-255. https://doi.org/10.1016/j.yqres.2004.07.001
• Merow C, Silander J (2014) A comparison of Maxlike and Maxent for modelling species distributions. Methods in Ecology and Evolution 5 (3): 215-225. https://doi.org/10.1111/2041-210x.12152
• Meyer de Schauensee R (1964) The birds of Colombia and adjacent areas of South and Central America. The Academy of Natural Sciences of Philadelphia, Philadelphia, 460 pp.
• Meyer de Schauensee R (1982) A guide to the birds of South America. The Academy of Natural Sciences of Philadelphia, Philadelphia, 498 pp.
• Meyer de Schauensee R, Phelps WHJ (1978) A Guide to the Birds of Venezuela. 1st. Princeton University Press, Princeton, 424 pp.
• Montgomery D, Balco G, Willett S (2001) Climate, tectonics, and the morphology of the Andes. Geology 29 (7): 579-582. https://doi.org/10.1130/0091-7613(2001)029<0579:CTTAMO>2.0.CO;2
• Muenchow J, Wehrden Hv, Rodríguez EF, Arisméndiz RR, Bayer F, Richter M (2013) Woody vegetation of a Peruvian tropical dry forest along a climatic gradient depends more on soil than annual precipitation. Erdkunde 67 (3): 241-248. https://doi.org/10.3112/erdkunde.2013.03.03
• Muñoz-Ortiz A, Velásquez-Álvarez ÁA, Guarnizo C, Crawford A (2014) Of peaks and valleys: testing the roles of orogeny and habitat heterogeneity in driving allopatry in mid-elevation frogs (Aromobatidae: Rheobates) of the northern Andes. Journal of Biogeography 42 (1): 193-205. https://doi.org/10.1111/jbi.12409

• Muñoz P, Gorín G, Parra N, Velásquez C, Lemos D, Monsalve-M. C, Jojoa M (2017) Holocene climatic variations in the Western Cordillera of Colombia: A multiproxy high-resolution record unravels the dual influence of ENSO and ITCZ. Quaternary Science Reviews 155: 159-178. https://doi.org/10.1016/j.quascirev.2016.11.021

• Nenzén HK, Araújo MB (2011) Choice of threshold alters projections of species range shifts under climate change. Ecological Modelling 222 (18): 3346-3354. https://doi.org/10.1016/j.ecolmodel.2011.07.011

• Norris D (2014) Model thresholds are more important than presence location type: understanding the distribution of lowland tapir (Tapirus terrestris) in a continuous Atlantic forest of Southeast Brazil. Tropical Conservation Science 7 (3): 529-547. https://doi.org/10.1177/194008291400700311

• Olivares A (1996) Adiciones a la avifauna colombiana, IV (Apodidae-Picidae). Hornero 10: 403-435. [In Spanish].

• Olson D, Dinerstein E, Wikramanayake E, Burgess N, Powell GN, Underwood E, D'amico J, Itoua I, Strand H, Morrison J, Loucks C, Allnutt T, Ricketts T, Kura Y, Lamoreux J, Wettengel W, Hedao P, Kassem K (2001) Terrestrial ecoregions of the World: a new map of Life on Earth. BioScience 51 (11): 933-93. https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

• Paradis E (2012) Analysis of Phylogenetics and Evolution with R. Springer-Verlag, New York, 386 pp. https://doi.org/10.1007/978-1-4614-1743-9

• Paradis E, Claude J, Strimmer K (2004) APE: Analyses of Phylogenetics and Evolution in R language. Bioinformatics 20 (2): 289-290. https://doi.org/10.1093/bioinformatics/btg412

• Patton JL, da Silva MF (1998) Rivers, refuges, and ridges: the geography of speciation of Amazonian mammals. In: Howard DJ, Berlocher SH (Eds) Endless forms: species and speciation. Oxford University Press, New York, 470 pp. [ISBN 0195109015].

• Pearson R, Raxworthy C, Nakamura M, Peterson AT (2006) Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. Journal of Biogeography 34 (1): 102-117. https://doi.org/10.1111/j.1365-2699.2006.01594.x

• Peraza C (2011) Aves, Bosque Oriental de Bogotá Protective Forest Reserve, Bogotá, D.C., Colombia. Check List 7 (1): 57-63. https://doi.org/10.15560/7.1.57

• Peraza PA (2008) Soil fertility and arboreal mammal biomass in tropical forest. In: Carson W, Schnitzer S (Eds) Tropical Forest Community Ecology. John Wiley and Sons Ltd, Chichester, 536 pp. [ISBN 978-1-4051-8952-1].

• Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2012) Ecological niches and geographic distributions. Princeton University Press, Princeton, 328 pp. [ISBN 9781400840670]

• Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259. https://doi.org/10.1016/j.ecolmodel.2005.03.026
• Phillips S, Dudík M, Schapire R (2004) A maximum entropy approach to species distribution modelling. Twenty-first international conference on Machine learning - ICML '04, 21 https://doi.org/10.1145/1015330.1015412

• Polissar P, Abbott M, Wolfe A, Vuille M, Bezada M (2013) Synchronous interhemispheric Holocene climate trends in the tropical Andes. Proceedings of the National Academy of Sciences 110 (36): 14551-14556. https://doi.org/10.1073/pnas.1219681110

• Polissar PJ, Abbott MB, Wolfe AP, Bezada M, Rull V, Bradley RS (2006) Solar modulation of Little Ice Age climate in the tropical Andes. Proceedings of the National Academy of Sciences 103 (24): 8937-8942. https://doi.org/10.1073/pnas.0603118103

• Pomara L, Ruokolainen K, Tuomisto H, Young K (2012) Avian composition co-varies with floristic composition and soil nutrient concentration in Amazonian upland forests. Biotropica 44 (4): 545-553. https://doi.org/10.1111/j.1744-7429.2011.00851.x

• Poor E, Loucks C, Jakes A, Urban D (2012) Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. PLoS ONE 7 (11): e49390. https://doi.org/10.1371/journal.pone.0049390

• Prum RO (1988) Historical relationships among avian forest areas of endemism in the Neotropics. In: Ouellet H (Ed.) Acta XIX Congressus Internationalis Ornithologici. 1. University of Ottawa Press, Ottawa, 2400 pp. [ISBN 0776601962].

• Ramírez-Barahona S, Euquaire L (2013) The role of glacial cycles in promoting genetic diversity in the Neotropics: the case of cloud forests during the Last Glacial Maximum. Ecology and Evolution 3 (3): 725-738. https://doi.org/10.1002/eee3.483

• Ramoni-Perazzi P, Muñoz-Romo M, Chaves LF, Kunz T (2012) Range prediction for the giant fruit-eating bat, Artibeus amplus (Phyllostomidae: Stenodermatinae) in South America. Studies on Neotropical Fauna and Environment 47 (2): 87-103. https://doi.org/10.1080/01650521.2012.679485

• Ramos Pereira MJ, Marques JT, Santana J, Santos CD, Valsecchi J, de Queiroz HL, Beja P, Palmeirim J (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. Journal of Animal Ecology 78 (6): 1163-1171. https://doi.org/10.1111/j.1365-2656.2009.01591.x

• Ray N, Adams JM (2001) A GIS-based vegetation map of the world at the Last Glacial Maximum (25,000-15,000 BP). Internet Archeology 11.

• Restall R, Rodner C, Lentino M (2006) Birds of Northern South America: an identification guide. 1. Yale University Press, New Haven, 880 pp. [ISBN 0300108621]

• Restrepo JJ, Toussaint JF (1988) Terranes and continental accretion in the Colombian Andes. Episodes 7: 189-193.

• Restrepo-Pace P, Ruiz J, Gehrels G, Cosca M (1997) Geochronology and Nd isotopic data of Grenville-age rocks in the Colombian Andes: new constraints for late Proterozoic-early Paleozoic paleocontinental reconstructions of the Americas. Earth and Planetary Science Letters 150: 427-441. https://doi.org/10.1016/s0012-821x(97)00091-5

• Rissler L, Apodaca J, Weins J (2007) Adding More Ecology into Species Delimitation: Ecological Niche Models and Phylogeography Help Define Cryptic Species in the Black Salamander (Aneides flavipunctatus). Systematic Biology 56 (6): 924-942. https://doi.org/10.1080/10635150701703063

• Rull V, Schubert C (1989) The little ice age in the tropical Venezuelan Andes. Acta Científica Venezolana 40: 71-73.
• Rull V, Salgado-Labouriau ML, Schubert C, Valastro S (1987) Late holocene temperature depression in the Venezuelan andes: Palynological evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 60: 109-121. https://doi.org/10.1016/0031-0182(87)90027-7

• Salo J (1987) Pleistocene forest refuges in the Amazon: evaluation of the biostratigraphical, lithostratigraphical and geomorphological data. Annales Zoologici Fennici 24: 203-211.

• Scheffers B, Yong DL, C. Harris JB, Giam X, Sodhi N (2011) The World’s Rediscovered Species: Back from the Brink? PLoS ONE 6 (7): e22531. https://doi.org/10.1371/journal.pone.0022531

• Schenk CJ, Viger RJ, Anderson CP (1999) Maps showing geology, oil and gas fields, and geologic provinces of South America. Open-File Report 97-470D. US Geological Service. URL: http://pubs.usgs.gov/of/1997/ofr-97-470/OF97-470D/

• Schluter D (2000) The ecology of adaptive radiation. Oxford University Press, Oxfor, 296 pp. [In English]. [ISBN 9780198505228]

• Schluter D (2001) Ecology and the origin of species. Trends in Ecology & Evolution 16 (7): 372-380. https://doi.org/10.1016/s0169-5347(01)02198-x

• Schuchmann K, Weller A, Heynen I (2001) Systematics and biogeography of the Andean genus Eriocnemis (Aves: Trochilidae). Journal für Ornithologie 142 (4): 433-481. https://doi.org/10.1046/j.1439-0361.2001.01025.x

• Schuchmann KL (1999) Family Trochilidae (Hummingbirds). In: del Hoyo J, Elliot A, Sargatal J (Eds) Handbook of the birds of the world. Volume 5: Barn-owls to hummingbirds. Lynx Edicions, Barcelona, 759 pp. [ISBN 84-87334-25-3].

• Sclater PL, Salvin O (1868) On Venezuelan birds collected by Mr. A. Goering. Part I. Proceedings of the Zoological Society of London 1868: 165-173.

• Sclater PL, Salvin O (1870) On Venezuelan birds collected by Mr. A. Goering. Part IV. Proceedings of the Zoological Society of London 1870: 779-788.

• Sclater PL, Salvin O (1875) On Venezuelan birds collected by Mr. A. Goering. Part V. Proceedings of the Zoological Society of London 1875: 234-238.

• Sigrist MS, de Carvalho CJB (2009) Historical relationships among areas of endemism in the tropical South America using Brooks Parsimony Analysis (BPA). Biota Neotropica 9 (4): 79-90. https://doi.org/10.1590/s1676-06032009000400009

• Silva D, Vilela B, Marco PD, Nemésio A (2014) Using ecological niche models and niche analyses to understand speciation patterns: the case of sister Neotropical orchid bees. PLoS ONE 9 (11): e113246. https://doi.org/10.1371/journal.pone.0113246

• Simpson Vuilleumier BS (1971) Pleistocene changes in the fauna and flora of South America. Science 173 (3999): 771-780. https://doi.org/10.1126/science.173.3999.771

• Spence JM (1878) The land of Bolivar: or, war, peace and adventure in the Republic of Venezuela. S. Low, Marston, Searle and Rivington, London, 378 pp.

• Starrfelt J, Kokko H (2012) Bet-hedging—a triple trade-off between means, variances and correlations. Biological Reviews 87 (3): 742-755. https://doi.org/10.1111/j.1469-185x.2012.00225.x

• Stine B, Wagner W (2005) Plant extinctions: chiaroscuro in shades of green. In: Krupnick GA, Kress WJ (Eds) Plant conservation: A natural history approach. 1st. University of Chicago Press, Chicago, 346 pp. [ISBN 0226455122].
• Sullivan B, Wood C, Iliff M, Bonney R, Fink D, Kelling S (2009) eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation 142 (10): 2282-2292. https://doi.org/10.1016/j.biocon.2009.05.006
• Syfert M, Smith M, Coomes D (2013) The effects of sampling bias and model complexity on the predictive performance of maxEnt species distribution models. PLoS ONE 8 (2): e55158. https://doi.org/10.1371/journal.pone.0055158
• Symula R, Schulte R, Summers K (2003) Molecular systematics and phylogeography of Amazonian poison frogs of the genus Dendrobates. Molecular Phylogenetics and Evolution 26 (3): 452-475. https://doi.org/10.1016/s1055-7903(02)00367-6
• Taboada A, Rivera L, Fuenzalida A, Cisternas A, Philip H, Bijwaard H, Olaya J, Rivera C (2000) Geodynamics of the northern Andes: subductions and intracontinental deformation (Colombia). Tectonics 19 (5): 787-813. https://doi.org/10.1029/2000tc900004
• Taylor MA, Alfaro EJ (2005) Central America and the Caribbean, Climate of. In: Oliver JE (Ed.) Encyclopedia of World Climatology. 1st Edition. Springer, Dordrecht, 854 pp. [ISBN 1402032641].
• Terribile L, Diniz-Filho J, Marco Jr. PD (2010) How many studies are necessary to compare niche-based models for geographic distributions? Inductive reasoning may fail at the end. Brazilian Journal of Biology 70 (2): 263-269. https://doi.org/10.1590/s1519-69842010000200005
• Tingley R, Herman TB (2009) Land-cover data improve bioclimatic models for anurans and turtles at a regional scale. Journal of Biogeography 36 (9): 1656-1672. https://doi.org/10.1111/j.1365-2699.2009.02117.x
• Tuomisto H, Ruokolainen K (1997) The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. Biodiversity and Conservation 6 (3): 347-357. https://doi.org/10.1023/a:1018308623229
• Unger M, Homeier J, Leuschner C (2012) Effects of soil chemistry on tropical forest biomass and productivity at different elevations in the equatorial Andes. Oecologia 170 (1): 263-274. https://doi.org/10.1007/s00442-012-2295-y
• Valencia BG, Urrego DH, Silman MR, Bush MB (2010) From ice age to modern: a record of landscape change in an Andean cloud forest. Journal of Biogeography 37 (9): 1637-1647. https://doi.org/10.1111/j.1365-2699.2010.02318.x
• van der Hammen T (1974) The Pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1 (1): 3-2. https://doi.org/10.2307/3038066
• VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2014) SDMTools: species distribution modelling tools. Tools for processing data associated with species distribution modelling exercises. 1.1-221. The Comprehensive R Archive Network. Release date: 2014-8-05. URL: http://www.rforge.net/SDMTools/
• Vanzolini PE (1988) Distribution patterns of South American lizards. Workshop on Neotropical Distribution Patterns, Rio de Janeiro, 12-16 January 1987. Academia Brasileira de Ciências, Rio de Janeiro, 488 pp.
• Varela S, Anderson R, García-Valdés R, Fernández-González F (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37: 1084-109. https://doi.org/10.1111/j.1600-0587.2013.00441.x
• Vuilleumier F (1969) Field notes on some birds from the Bolivian Andes. Ibis 111 (4): 599-608. https://doi.org/10.1111/j.1474-919x.1969.tb02569.x
• Vuilleumier F (1984) Faunal turnover and development of fossil avifaunas in South America. Evolution 38 (6): 1384-1396. https://doi.org/10.1111/j.1558-5646.1984.tb05659.x

• Vuilleumier F, Simberloff D (1980) Ecology versus history as determinants of patchy and insular distributions in high Andean birds. In: Hecht MK, Steere WC, Wallace B (Eds) Evolutionary biology. 12. Plenum Press, New York, 388 pp. [ISBN 978-1-4615-6961-9].

• Warren D (2012) In defense of ‘niche modeling’. Trends in Ecology & Evolution 27 (9): 497-500. https://doi.org/10.1016/j.tree.2012.03.010

• Weller AA, Schuchmann KL (2004) Biogeographic and taxonomic revision of the trainbearers Lesbia (Trochilidae) with the description of two new subspecies. Ornithologischer Anzeiger 43 (2): 115-136.

• Wielstra B, Beukema W, Arntzen J, Skidmore A, Toxopeus A, Raes N (2012) Corresponding mitochondrial DNA and niche divergence for Crested Newt candidate species. PLoS ONE 7 (9): e46671. https://doi.org/10.1371/journal.pone.0046671

• Willis EO, Schuchmann KL (1993) Comparison of cloud-forest avifaunas in southeastern Brazil and western Colombia. Ornitología Neotropical 4: 55-63.

• Zhang Y, Chen C, Li L, Zhao C, Chen W, Huang Y (2014) Insights from ecological niche modeling on the taxonomic distinction and niche differentiation between the black-spotted and red-spotted tokay geckoes (Gekko gecko). Ecology and Evolution 4 (17): 3383-3394. https://doi.org/10.1002/ece3.1183

• Zimmer JT (1951) Studies of Peruvian birds. No. 61. The genera Aglaeactis, Lafresnaya, Pterophanes, Boissonneaua, Heliangelus, Eriocnemis, Haplophaedia, Ocreatus, and Lesbia . American Museum Novitates 1540: 1-5.

• Züchner T, Boesman P, Kirwan GM (2017) Green-tailed Trainbearer (Lesbia nuna). http://www.hbw.com/node/55603. Accessed on: 2017-4-23.