



Acta Biológica Colombiana

ISSN: 0120-548X

Universidad Nacional de Colombia, Facultad de Ciencias,
Departamento de Biología

ACEVEDO, Aldemar A.; ARMESTO SANGUINO, Orlando; OLARTE
QUINÓNEZ, Camilo Andrés; SOLANO, Liliana; ALBORNOZ ESPINEL, Mónica
María; CABRERA, James Alexis; CARRERO SARMIENTO, Diego Armando
POTENTIAL SPECIES RICHNESS OF FROGS AND DIURNAL BUTTERFLIES IN THREE
BIOGEOGRAPHICAL UNITS FROM NORTHEASTERN COLOMBIA: CONSERVATION IMPLICATIONS
Acta Biológica Colombiana, vol. 23, no. 2, 2018, May-September, pp. 151-162
Universidad Nacional de Colombia, Facultad de Ciencias, Departamento de Biología

DOI: <https://doi.org/10.15446/abc.v23n2.65300>

Available in: <https://www.redalyc.org/articulo.oa?id=319057945002>

- How to cite
- Complete issue
- More information about this article
- Journal's webpage in [redalyc.org](https://www.redalyc.org)

 [redalyc.org](https://www.redalyc.org)

Scientific Information System Redalyc
Network of Scientific Journals from Latin America and the Caribbean, Spain and
Portugal

Project academic non-profit, developed under the open access initiative



POTENTIAL SPECIES RICHNESS OF FROGS AND DIURNAL BUTTERFLIES IN THREE BIOGEOGRAPHICAL UNITS FROM NORTHEASTERN COLOMBIA: CONSERVATION IMPLICATIONS

Riqueza potencial de las especies de ranas y mariposas diurnas en tres unidades biogeográficas del nororiente de Colombia: implicaciones para la conservación

Aldemar A. ACEVEDO^{1,2}, Orlando ARMESTO SANGUINO^{1,2}, Camilo Andrés OLARTE QUIÑÓNEZ², Liliana SOLANO³, Mónica María ALBORNOZ ESPINEL², James Alexis CABRERA^{2,4}, Diego Armando CARRERO SARMIENTO².

¹ Laboratorio de Biología Evolutiva, Pontificia Universidad Católica de Chile. Avenida Libertador Bernardo O'Higgins 340. Santiago, Chile.

² Grupo de Investigación en Ecología y Biogeografía, Universidad de Pamplona. Barrio El Buque, Km 1, Vía a Bucaramanga. Pamplona, Colombia.

³ Grupo de Investigación Biología Evolutiva, Universidad de Sucre. Cra 28 No. 5-267 Barrio Puerta Roja. Sincelejo, Colombia.

⁴ Programa de Biología, Universidad del Tolima. Barrio Santa Helena Parte Alta. Ibagué, Colombia.

For correspondence. aeacevedo@uc.cl

Received: 27th May 2017, **Returned for revision:** 22nd November 2017, **Accepted:** 14th December 2017.

Associate Editor: Martha Ramírez Pinilla.

Citation/Citar este artículo como: Acevedo AA., Armesto Sanguino O, Olarte Quiñónez CA, Solano L, Albornoz Espinel MM, Cabrera JA, Carrero Sarmiento DA. Potential species richness of frogs and diurnal butterflies in three biogeographical units from northeastern Colombia: conservation Implications. Acta biol. Colomb. 2018;23(2):151-162. DOI:<http://dx.doi.org/10.15446/abc.v23n2.65300>

ABSTRACT

We present an estimation of the potential species richness of frogs, and diurnal butterflies distributed in the departments of Norte de Santander and Santander, Colombia, and analyze the implications for conservation of such high Andean species. From June 2012 to May 2016, we sampled across the Almorzadero, Santurbán and Tamá biogeographical units to gather presence data of 7 anuran species and 29 butterflies species from the superfamily Papilionoidea. We modeled the potential distribution of each species, converted every model to binary, and the sum up of unique species per cell allowed to estimate the model of potential richness, generating the total number of species for every 1 km² cell. Every model was validated against field data, vegetation cover, and altitude. Our results suggest the existence of species' concentration zones, specifically in the places of convergence between biogeographical units; it was evident the high levels of data deficiency in some places. Finally, it was clear the importance of these zones as a continuum of biogeographic conditions to maintain the biological diversity.

Keywords: biogeography, biological diversity, conservation, high Andean species, species distribution models.

RESUMEN

Presentamos una estimación de la riqueza potencial y las implicaciones para la conservación de especies altoandinas de anuros y de mariposas diurnas, distribuidas en los departamentos de Norte de Santander y Santander. Durante junio de 2012 y mayo de 2016 se realizaron muestreos de campo en las unidades biogeográficas de Almorzadero, Santurbán y Tamá, para registrar los datos de presencia de siete especies de anfibios del orden Anura y 29 de mariposas de la superfamilia Papilionoidea. Realizamos modelamientos de la distribución potencial de cada especie, convertimos cada modelo en binario, y la suma de especies únicas por celda permitió estimar el modelo de riqueza potencial, obteniendo el número total de especies por cada celda de 1 km²; a su vez, los modelos fueron superpuestos sobre información de campo, cobertura vegetal y altitudinal. Nuestros resultados sugieren que existen zonas concretas de concentración de especies en las zonas de convergencia entre las unidades biogeográficas, así como zonas con vacíos de información. Resaltamos la importancia de estas zonas como un continuo de condiciones biogeográficas para mantener la diversidad.

Palabras clave: biogeografía, conservación, diversidad biológica, especies altoandinas, modelo de distribución de especies.

INTRODUCTION

Colombia is a mega-diverse country; it harbors one of the highest diversities of fauna and flora in the world (Rangel-Ch., 2015). However, its strategic location in the northern Andes implies a very rapid landscape transformation and biodiversity loss (Armenteras *et al.*, 2003); even so the tropical Andes are a priority for conservation due to their high levels of diversity and endemism (Myers *et al.*, 2000; Pennington *et al.*, 2010). Moreover, the Andes harbor a wide variety of ecosystems, from Andean and high Andean forests to paramos (Rodríguez *et al.*, 2006); the latter, are especially interesting as they generate a particular pattern: many species occupy narrow altitudinal ranges (Terborgh, 1992; Bernal and Lynch, 2008).

In Colombia, the Andes split into three cordilleras: Occidental, Central, and Oriental. The latter has the largest geographic extension, and it harbors four biogeographical units: Santurbán, Almorzadero, Tamá, and Yariguíes, which constitute an important ecological zone that acts as natural reserve and source of hydrological resources for two departments, Norte de Santander and Santander (Morales *et al.*, 2007). Nevertheless, a great area of these biogeographical units has never been studied or remains poorly explored, and therefore the knowledge about its biodiversity is scarce (Acevedo *et al.*, 2016a).

The Andean ecosystems are characterized by high levels of species richness and endemism (Myers *et al.*, 2000; Herzog *et al.*, 2011). Taxonomic groups well represented in such habitats are amphibians and insects; the former group comprises frogs and toads that belong to the order Anura, which contains the majority of species of amphibians compared to the other two orders (Caudata, salamanders, and Apoda, caecilians). There are 754 species of the order Anura in Colombia (Acosta, 2017), 396 of which inhabit the Cordillera Oriental (Bernal and Lynch, 2008); in such mountain ranges some groups of amphibians exhibit marked diversification patterns, such as the genera *Pristimantis* (family Craugastoridae), *Dendropsophus* (Hylidae) and *Gastrotheca* (Hemiphractidae) (Lynch, 1998; Meza-Joya and Torres, 2016; Armesto and Señaris, 2018).

Meanwhile, Andean butterflies are mainly represented by the superfamily Papilionoidea, particularly the subtribe Pronophilina, which is one of the most diverse groups of butterflies in the Andean and high Andean ecosystems (Mahecha-Jiménez *et al.*, 2011). There are roughly 520 species of this subtribe (Lamas *et al.*, 2004; Pyrcz *et al.*, 2011) and 205 occur in Colombia, which has the second highest richness of Pronophilina in the Andes (Lamas *et al.*, 2004; Pyrcz and Rodríguez, 2007). Moreover, these butterflies can act as indicators of diversity due to their level of endemism in the high Andean region (Pyrcz and Rodríguez, 2007), promoted by their specialized diets based on plant families like Poaceae, Marantaceae, Arecaceae and Cyperaceae (García-Perez *et al.*, 2007; Pyrcz and Vilorio, 2007).

Species distribution models (SDMs)

The presence of a species is determined by several factors operating at different levels of intensity and scale (Pearson and Dawson, 2003), which are represented by environmental aspects including climatic and habitat conditions, as well as ecological factors related to competition, predation, and parasitism (Ortiz-Yusty *et al.*, 2014).

There are two approaches to species distribution, one theoretical and one practical: the actual distribution, which relates to the occurrence of the species represented by the geographical localities where individuals of the species have been recorded. The potential distribution, related to areas that have very similar environmental conditions to the sites where the species already occurs, and therefore such potential areas have very high probabilities of being occupied by the same species (Gámez, 2011). It is common to have incomplete data on the distribution of species and often such data only covers presence data (Pearson *et al.*, 2007). Therefore, the need to generate models that allow us to infer the distribution patterns to extrapolate the information into ecological, evolutionary or conservation contexts.

Niche modeling is an increasingly used tool to estimate the potential distribution of species (Lobo *et al.*, 2010); such models estimate the potential distribution by correlating occurrence information with environmental predictors. Moreover, ecological niches refer to the relationships between environmental variables, which offer the ecological conditions necessary to the development and long-term survival of a particular species (Soberón and Peterson, 2005). Studies focusing on the comparison of different methods for niche modeling indicate that MaxEnt, based on the algorithm of maximum entropy (Phillips *et al.*, 2006), is one of the most robust methods (Tognelli *et al.*, 2009). Moreover, it only requires presence data and environmental variables, and it does not lose robustness when working with small data sets (Figueroa *et al.*, 2016). MaxEnt provides response curves for every species about environmental variables and estimates the importance of each variable in explaining the distribution of the species. To validate the obtained model MaxEnt uses the criteria of the area under the curve (AUC), derived from the curve operated by the receptor (ROC) (Phillips *et al.*, 2006). These kind of models have multiple applications: detection of new areas of distribution and new species (Pearson *et al.*, 2007); studies about potential impacts of climate change (Levinsky *et al.*, 2007); prediction of biological invasions and expansion of biological vectors and pathogens (Ward, 2007); design of conservation strategies (Ferrier, 2002), to name but a few.

The importance of conserving the Andean ecosystems is evident; however, there is a lack of information about the conservation status in northeastern Colombia and their fauna. Therefore, this study aimed to determine the patterns

of species potential richness and their implications for the conservation of frogs and diurnal butterflies along three biogeographical zones of northeastern Colombia.

MATERIALS AND METHODS

Study area

From June 2012 to May 2016, we sampled different locations from the biogeographical units: Santurbán (Norte de Santander) (five locations), Almorzadero (Santander and Norte de Santander) (seven locations), and Tamá (Norte de Santander) (six locations) (Fig. 1), covering an altitudinal gradient from 2000 to 3800 m a.s.l.

The biogeographical units Almorzadero, Santurbán, and Tamá are located along the northeastern area of the Cordillera

Oriental in Colombia. All three units have orobiomes corresponding to Andean, Highandean, Subparamo, and Paramo, with conditions of precipitation ranging from humid to very humid. The regime of precipitations is bimodal, with two dry periods and two rainy seasons; minimum precipitation is 600 mm, and the maximum levels per zone are 1379 mm in Almorzadero; 1567 mm in Tamá and 2500 mm in the Santurbán; mean multiannual temperature oscillate between 6 and 13.5 °C (Morales *et al.*, 2007).

Vegetation exhibits a high abundance of the families Asteraceae, Poaceae, Rosaceae, Scrophulariaceae, Ericaceae, Melastomataceae; and species of the genera *Lachemillam*, *Hypericum*, *Baccharis*, *Carex*, *Castilleja*, *Chaetopelis*, *Tamania*, *Libanothamnus*, *Rulopezia*, *Espeletiopsis*, *Ageratina*, *Calamagrostis*, *Agrostis*, *Chusquea* and *Espeletia* (Rangel-Ch., 2000).

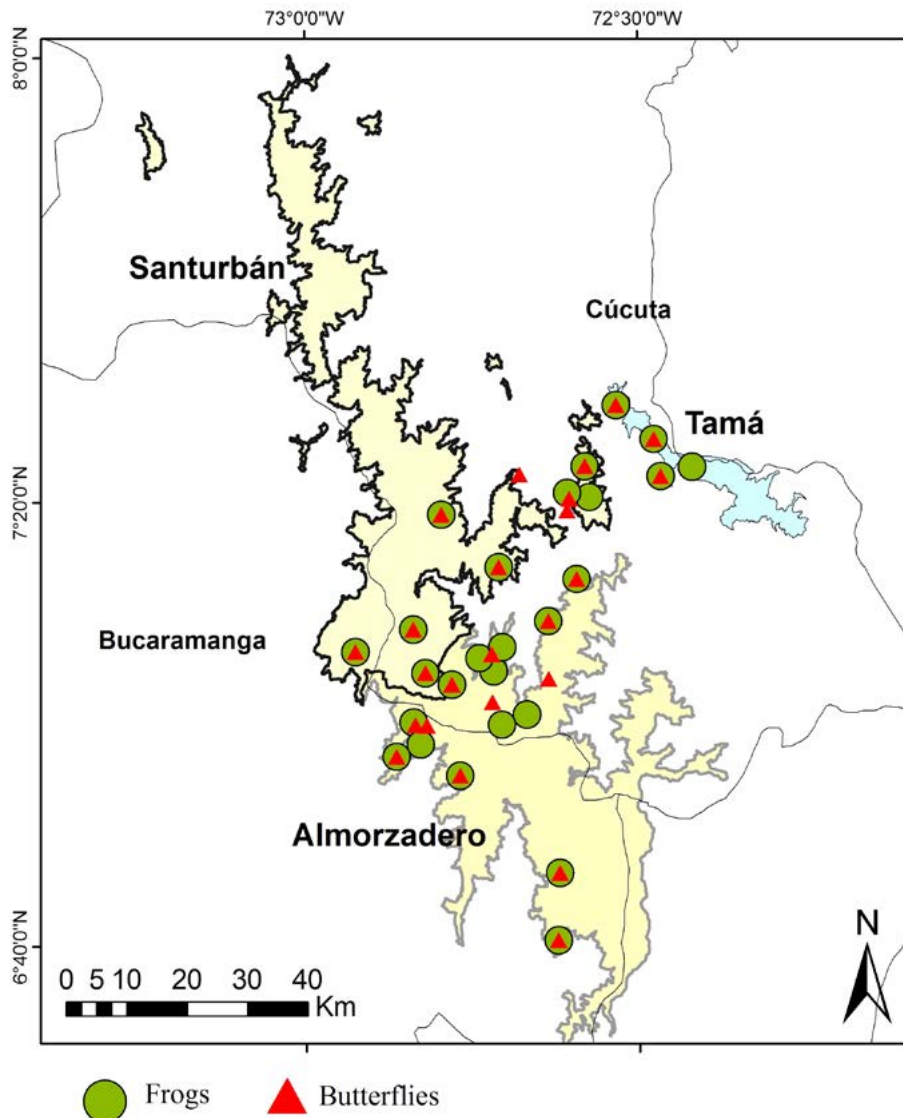


Figure 1. Study area, showing the geographic limits between Almorzadero, Tamá and Santurbán biogeographical units, Norte de Santander-Santander, Colombia.

The three biogeographical units suffer a high anthropic intervention, particularly due to the establishment of grasslands and crops like potato, onions, beans, and corn; moreover, there are areas dedicated to cattle ranching of ovine, bovine, equine and porcine. Also, the establishment of gold and silver mining directly causes a rapid loss of habitat, affecting the plant and animal species (Morales *et al.*, 2007).

Sampling methods

Amphibians

The collection of amphibians consisted of random walks by two observers applying the technique of visual encounter (Crump and Scott, 1994), from 18:00 h to 22:00 h. Surveys included all the different available microhabitats (rocks; dead logs; streams' borders; bryophytes; grass; *frailejón* (characteristic paramo's plants); bromeliads; tree trunks and shrubs; under and on the leaf litter). Information registered for every individual consisted of geographical, environmental, and ecological data: date and time of capture, altitude, geographic coordinates, type of vegetation cover, environmental temperature, relative humidity, type of substrate and height to the position of the individual, and activity.

Butterflies

For the collection of butterflies, using entomological nets, random field stations were located following an altitudinal gradient of 500 m (Ríos-Málaver, 2007; Van Swaay *et al.*, 2015). In every station, three people performed random walks between 08:00 h and 17:00 h, with a sampling effort of 9 hrs/day/person (Villareal *et al.*, 2004); the aims were to sample the different altitudes along the gradient, to cover every type of flight habit of the butterflies and to take advantage of the daylight (Gaviria-Ortiz and Henao-Bañol,

2011). The time of collection of butterflies varied from day to day among the stations, in order to contemplate the spatial and temporal differences along the gradient (Carrero *et al.*, 2013). Samples were stored in individual envelopes, labeled with the following data: locality, data, time, and sampling station of capture; the samples remained cool until the preparation, preservation and taxonomic determination in the laboratory (Andrade *et al.*, 2013). In addition, the information regarding the sampling station was recorded in a field book.

Most of the records obtained in this study are currently a repository in the Sistema de Información de Biodiversidad (SIB-Colombia) under the certifications 15825BEBD9E (amphibians) and 15820B48580 (butterflies).

Species distribution models (SDMs)

We generated occurrence maps of amphibians and butterflies based on the data gathered in the field, and in an occurrence search conducted by reviewing scientific publications, original descriptions, online databases (IUCN, HerpNet, GBIF, Scientific collections online-Universidad Nacional de Colombia, SiB Colombia); and an on-site revision of the biological collection of amphibians of the Instituto de Ciencias Naturales at the Universidad Nacional de Colombia and the Entomological Collection of the Universidad de Pamplona. Records of occurrence included frogs belonging to the genera: *Dendropsophus* (one species: 35 presence records), *Gastrotheca* (one species: 22 presence records), *Pristimantis* (four species: 84 presence records), and *Tachiramantis* (one species: 17 presence records) and for every species of diurnal butterflies (29 species: 266 presence records) (Table 1). The minimum number of presence records for a species was four.

Table 1. Species of frogs and butterflies from the Almorzadero, Santurbán, and Tamá biogeographical units included in the estimated species richness.

Species	Biogeographical units	Altitude m a.s.l.	Occurrences	Bioclimatic variables	AUC
Frogs					
<i>Pristimantis anolirex</i>	Almorzadero, Santurbán, Tamá	2600-3500	57	Bio1 Bio19	0.986
<i>Pristimantis nicefori</i>	Almorzadero, Tamá	3000-3500	14	Bio1 Bio19	0.992
<i>Pristimantis mondolfi</i>	Tamá	2100-2700	4	Bio19 Bio5	0.967
<i>Pristimantis</i> sp.	Almorzadero, Tamá	2900-3100	9	Bio19 Bio1	0.989
<i>Tachiramantis douglasi</i>	Almorzadero, Santurbán, Tamá	1800-2700	17	Bio1 Bio19	0.920
<i>Gastrotheca helenae</i>	Tamá	2700-3600	22	Bio19 Bio5	0.998
<i>Dendropsophus pelidna</i>	Almorzadero, Santurbán, Tamá	2000-3600	35	Bio1 Bio19	0.983

Species	Biogeographical units	Altitude m a.s.l.	Occurrences	Bioclimatic variables	AUC
Butterflies					
<i>Altopedaliodes cocytia</i>	Almorzadero, Santurbán, Tamá	2630-3540	30	Bio3 Bio5	0.993
<i>Altopedaliodes nebris</i>	Almorzadero, Santurbán	2860-3700	7	Bio3 Bio5	0.995
<i>Altopedaliodes tamaensis</i>	Almorzadero, Tamá	2770-3741	9	Bio1 Bio3	0.994
<i>Ancyloxypha melanoneura</i>	Almorzadero	2880-3400	5	Bio3 Bio5	0.989
<i>Catasticta cinerea</i>	Almorzadero, Santurbán	2607-3229	4	Bio5 Bio3	0.997
<i>Catasticta philais philais</i>	Almorzadero, Santurbán	2607-3200	6	Bio6 Bio3	0.996
<i>Colias dimera</i>	Almorzadero, Santurbán, Tamá	2490-3672	24	Bio5 Bio3	0.991
<i>Corades chelonis</i>	Almorzadero, Santurbán, Tamá	2490-2794	4	Bio19 Bio2	0.996
<i>Dalla hesperioides</i>	Almorzadero, Santurbán	2674-3229	8	Bio3 Bio6	0.993
<i>Dione glycera</i>	Almorzadero, Santurbán, Tamá	2607-3400	10	Bio5 Bio13	0.985
<i>Eretris apuleja</i>	Almorzadero	2607-3090	4	Bio3 Bio19	0.994
<i>Hemiargus hanno</i>	Almorzadero	2607-3229	4	Bio3 Bio5	0.988
<i>Idioneurula erebioides</i>	Almorzadero, Santurbán, Tamá	2490-3512	25	Bio3 Bio5	0.992
<i>Johnsonita pardoa</i>	Almorzadero, Santurbán, Tamá	2490-3013	4	Bio5 Bio2	0.995
<i>Lasiophila circe</i>	Almorzadero, Santurbán	2607-3060	10	Bio3 Bio6	0.997
<i>Leptophobia eleone</i>	Almorzadero, Santurbán	2607-2989	5	Bio3 Bio19	0.998
<i>Leptophobia gonzaga</i>	Almorzadero, Santurbán	2704-3118	4	Bio5 Bio3	0.998
<i>Linka lina</i>	Almorzadero	2987-3451	7	Bio3 Bio6	0.995
<i>Lymanopoda lecromi</i>	Almorzadero, Santurbán, Tamá	2560-3013	4	Bio5 Bio3	0.996
<i>Nathalis plauta</i>	Almorzadero	2699-3741	11	Bio6 Bio3	0.995
<i>Pedaliodes empusa</i>	Almorzadero, Santurbán, Tamá	2674-3118	12	Bio3 Bio6	0.997
<i>Pedaliodes montagna</i>	Almorzadero	2607-2943	4	Bio3 Bio19	0.999
<i>Pedaliodes polla</i>	Almorzadero, Santurbán	2607-3090	8	Bio3 Bio6	0.997
<i>Pedaliodes polusca</i>	Santurbán, Tamá	2490-2920	7	Bio2 Bio5	0.999
<i>Pedaliodes praemontagna</i>	Almorzadero, Santurbán, Tamá	2490-3090	8	Bio5 Bio3	0.994
<i>Pedaliodes reyi</i>	Almorzadero, Santurbán, Tamá	2490-3118	25	Bio6 Bio3	0.991
<i>Steroma bega</i>	Almorzadero, Santurbán, Tamá	2560-2800	4	Bio5 Bio3	0.996
<i>Tatochila xanthodice</i>	Almorzadero	2607-3451	4	Bio6 Bio3	0.991
<i>Vanessa braziliensis</i>	Almorzadero, Santurbán	2607-3400	9	Bio3 Bio6	0.991

We modeled the SDMs for every amphibian and butterfly species, using the maximum entropy algorithm as implemented in MaxEnt (Phillips *et al.*, 2006) and global bioclimatic variables from WorldClim with a resolution of 30 arc seconds (~1 km²) (Hijmans *et al.*, 2005). Given the multicollinearity of variables can result in an excessive adjustment during the modeling of species distribution (Pearson *et al.*, 2007), we eliminated the correlated variables based on a Spearman Rank Correlation.

For every species of amphibian and butterfly, we obtained a niche model with 80 % of the data used as training data and 20 % of the data used for assessment of the model (test data). The modeling consisted of 5000 iterations, using the default parameters in MaxEnt, except for choosing 'without extrapolation,' in order to avoid artificial projections from the extreme values of ecological variables (Elith *et al.*, 2011). To obtain the values of habitat adaptation (continuous probability from 0 to 1) we used the logistic format; such values were then converted into binary absence-presence values, based on the threshold value established for every model.

The performance assessment of every obtained model followed the criterion of commission and omission error in the area under the curve ROC/AUC (Manel *et al.*, 2001). The tool "Estimate Species Richness" (ESR) (Brown, 2014), implemented in ArcGIS 10.3 (ESRI, 2011), converted every model to binary, and the sum up of unique species per cell allowed to estimate the model of potential richness, generating the total number of species for every 1 km² cell. Finally, the results were validated using models of elevation, field data and vegetation cover layers (scale 1: 100000) (IDEAM, 2010).

RESULTS

The values of AUC for the SDMs of every species of butterfly and frog reached optimal values for both, the training data (> 0.9) and the test data (> 0.98) (Table 1). The most important predictors for most amphibians were the following climatic variables: BIO1 = Annual Mean Temperature, and BIO19 = Precipitation of Coldest Quarter (Table 1). For diurnal butterflies, the most important predictors were BIO3 = Isothermality (BIO2/BIO7) (* 100); BIO6 = Min Temperature of Coldest Month and, occasionally, BIO5 = Max Temperature of Warmest Month and BIO19 = Precipitation of Coldest Quarter (Table 1).

Frogs

Regarding the frogs, our findings indicated that the highest concentration of species (ESR of three to seven species) occurs between 1500 and 3000 m a.s.l. mainly towards the north, between the biogeographical units of Santurbán and Tamá (Fig. 2a). The Estimate Species Richness also projected the highest potential richness of species outside the biogeographical units studied here, in the Serranía de los Yariquíes and the Mérida Cordillera (Venezuela) from

1500 and 2000 m a.s.l. (Fig. 2a). This pattern may be due to the potential distribution of the species of *Pristimantis* we included because they were recorded at intermediate altitudes (Fig. 3a), which suggests the bioclimatic conditions required by these species are similar in areas lower and farer away than we initially considered.

Potentially propitious areas for the occurrence of the species of the family Craugastoridae, assessed here, are located in secondary and mature forests, and paramo. However, some of these zones exhibit high degree of fragmentation due to cattle ranching and agriculture, including the municipalities of Cucutilla and Mutiscua (Santurbán); the municipalities of Toledo and Chinácota (buffer zones of the Tamá), the villages of the municipality of Chitagá in Norte de Santander, and Guaca, in Santander (Almorzadero).

Butterflies

Regarding the potential richness of diurnal butterflies, the estimated ESR, ranging from 16 to 23 species, indicated the highest richness occurs above 3000 m a.s.l. (Fig. 2b). The species belonging to the genus *Altopedialodes* concentrated mainly in the border zone between the Almorzadero and Santurbán, and some areas in the municipalities of Toledo and Chinácota, in the Tamá. The Estimate Species Richness coincided with vegetation covers characteristic of shrubland, frailejones and the transition between the high Andean forest and the paramo. Some of these areas exhibit a high degree of fragmentation with perturbed areas where common species include: *Colias dimera*, *Idioneurula erebioides*, *Dalla hesperioides* and *Linka lina*; moreover, potential distribution models for these species overlap with altitudes from 2800 to 3600 m a.s.l., where the anthropic pressure is intense. However, some species like *Corades chelonis*, *Daedalma drusilla*, *Lasiophila circe*, *Lymanopoda lecromi*, *Ly. mirabilis*, *Ly. samius*, *Manerebia leaena*, *M. pluviosa* and *Neopedialodes philotera*, occur in areas with conserved vegetation covers, which coincide with the SDM obtained for every species and the ESR that converged in the conserved areas of the biogeographical units Almorzadero and Santurbán.

DISCUSSION

Frogs

The richness patterns observed in this study concur with the information available for the species of the family Craugastoridae, particularly the genus *Pristimantis* that accounts for around 500 species (AmphibiaWeb, 2018). This group has a high presence in the Andean region, although it has adapted to a great variety of ecosystems, from humid forests (Wang *et al.*, 2008) to Andean forests, and paramo (Heinicke *et al.*, 2007). Meza-Joya and Torres (2016), indicated that 311 species of *Pristimantis* inhabit the northern Andes, reaching an altitudinal distribution above 4500 m a.s.l. Fieldwork allowed us to identify the sympatric

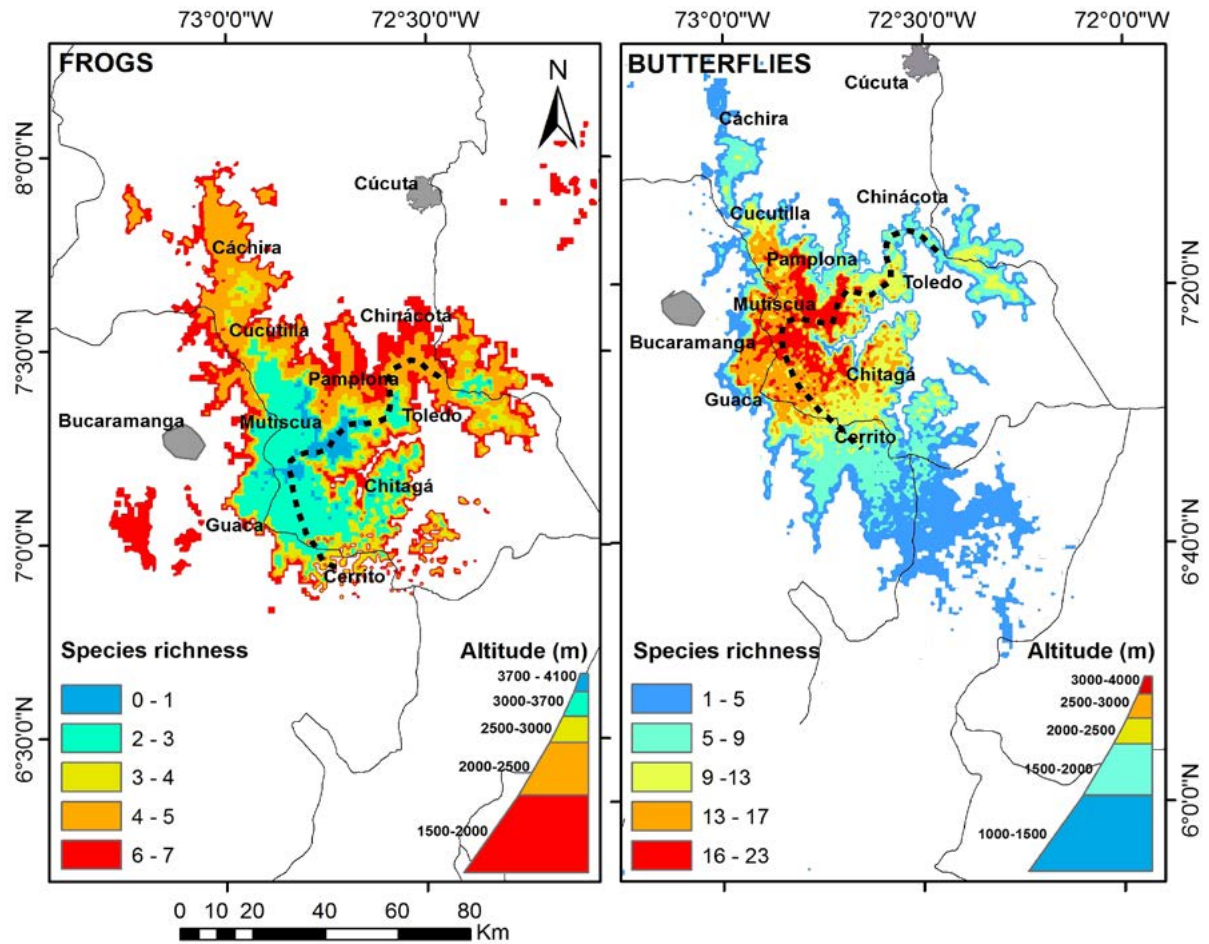


Figure 2. The estimated species richness (ESR) of frogs and diurnal butterflies in the different altitudes of the Almorzadero, Tamá, and Santurbán biogeographical units, Norte de Santander, Colombia. Discontinued line represents the zone of contact between the units.

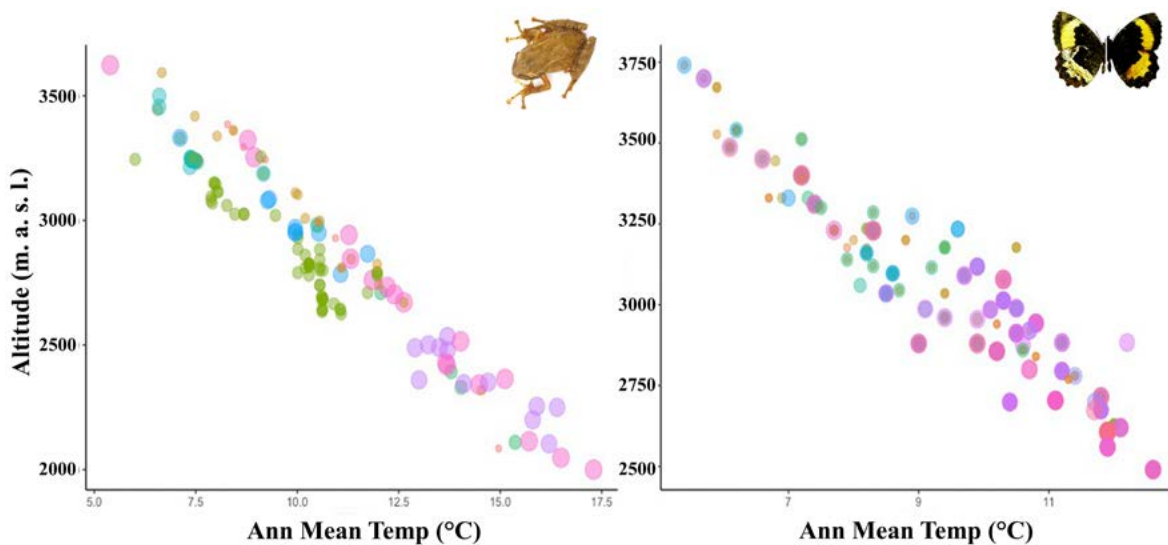


Figure 3. Distribution of amphibians and butterflies according to the altitudinal gradient and annual mean temperature (BIO1). Each color dot represents a species and the size the relative abundance.

distribution of *Tachiramantis douglasi* and *Pristimantis mondolfi* in this region (Fig. 3a) and the occurrence of a potentially new species of *Pristimantis*, mainly in the high Andean forest of the Tamá unit. In the high mountain, from 3500 to 3700 m a.s.l. (Fig. 3a), the ESR was three species, which matches previous observations in the area where we recorded three species of frogs: *Pristimantis anolirex*, *P. nicefori* and *Gastrotheca helenae* (Fig. 3a). Even so, these three species of frogs were associated to paramo in our study only *P. nicefori* and *G. helenae* have been previously identified as distinctive of the paramo (Lynch and Suárez-Mayorga, 2002).

The genera *Dendropsophus* and *Gastrotheca*, have lower presence in the Andes, but some species occur higher than 4000 m a.s.l.; therefore, the presence of these frogs in the high mountains suggests they may have adapted to particular ecosystems, such as the high Andean forest and the paramo, which could be associated to the conditions of the available habitats. For example, Andean species of *Dendropsophus* occur in lentic body waters, present in open and perturbed areas, as well as temporary and artificial ponds, usually in pastures far from the edge of the forest. Historical records of *D. pelidna* are as high as 3000 m a.s.l. (La Marca, 2004); it can inhabit the paramo and sub-paramo, but such distribution appears to be a recent invasion, similar to the documented in its closely related species *D. meridensis* in the Mérida Cordillera (Venezuela) (La Marca, 1994). In addition, this species is highly tolerant to habitat degradation and is capable of surviving in places where agrochemicals are intensely used (La Marca, 2004). During our fieldwork, we could confirm the latter, as individuals of *D. pelidna* were present in areas of paramo that have been modified into agriculture and, worth to mention, a frog was found at 3400 m a.s.l. of elevation into a container that had the remaining of a pesticide widely used for potato cultivation. This is an evidence of the problems that come along with the expansion of agriculture in the paramo, which can also trigger the spread of emergent diseases, such as chytridiomycosis in amphibians (Acevedo *et al.*, 2016a, Acevedo *et al.*, 2016b).

In contrast with the case above, *Gastrotheca helenae* inhabits the paramo Tamá, particularly the microhabitat offered by the frailejones, the mosses or some scrublands (Acevedo *et al.*, 2014). The bioecology of the species indicates that it is susceptible to habitat changes; in the paramo Tamá fires take place along with fast habitat fragmentation and cattle ranching (Acevedo *et al.*, 2011), despite being a protected area corresponding to the Tamá National Natural Park. Moreover, we have not found the species in any other biogeographical unit, so it has a very limited distribution, and its populations are threatened, which highlights the importance of strengthening and improving the programs for the conservation of habitats such as paramo (Albornoz *et al.*, 2017). We, therefore, suggest the need for urgent and efficient conservation measures in the region.

Butterflies

Direct associations between butterflies and the landscape demonstrate the importance of identifying areas of endemism, species exchange and patterns of the butterflies-host plant that are essential for sustaining and conserving the high mountain ecosystem structure (Viloria *et al.*, 2010; Marín *et al.*, 2015). Even so, the bioclimatic variables are highly determinant to infer potential distribution scenarios, it is also necessary to take into account different factors, like landscape transformation, land conversion into agriculture and cattle ranching, which are critical causes of reduction of the distribution areas for these insects (Romo *et al.*, 2013). These factors result in the loss of resources and reproduction zones for butterflies, which would make it difficult for species to adapt to climate change (Andrade and Amat, 1996; Andrade, 2011; Carrero *et al.*, 2013).

The distribution of groups like Hesperids, helps us to improve our knowledge about the state of poorly known species like *Ancyloxypha melanoneura*, *Dalla hesperioides*, and *Linka lina*, which are associated to perturbed vegetation covers; therefore, it highlights the importance of anthropically transformed areas to harbor high values of abundance, richness, and diversity of this family of butterflies (Obregón and Fernández, 2016).

Overall, in the high mountain butterflies' community, the subtribe Pronophilina was characterized by its richness (12 genera) and wide distribution, showing a correlation of the genera *Lasiophila*, *Lymanopoda*, *Neopedaliodes* and *Manerebia*, with covers of Andean forest; the genera *Corades* and *Pedaliodes*, were associated with transition areas, and the genus *Altopedaliodes* was restricted to the paramo. Checking up on the information about the altitudinal distribution of groups of butterflies like Pronophilina and Coliadinae they register an increase of their richness at elevations between 2800 and 3500 m a.s.l. (Fig. 3b); there is, therefore, a concentration of species at such elevation ranges benefited from the temperature that has generated scenarios of species replacement (Fig. 3b). The latter is a process that supports the butterflies' communities and their associations with the vegetation at higher elevation gradients, between 3200 and 4000 m a.s.l. (Pyrz *et al.*, 2009; Viloria *et al.*, 2010; Carrero *et al.*, 2013).

Species replacement environments and peaks of richness occur between 2800 and 3200 m a.s.l. (Fig. 3b), including summits and small-open areas perfect for the mating behavior and reproduction of butterflies, called "Hilltopping" (Shields, 1967; Alcock, 1987; Pe'er *et al.*, 2004; Prieto and Dahners, 2006). Moreover, these areas function as elements of increase of richness and conservation of the paramos, while promoting the spatial exchange between biogeographical units (Almorzadero, Santurbán y Tamá).

However, these Andean zones continue to undergo rapid processes of exploitation, human colonization and urbanization, fragmentation, deforestation and extraction

of non-timber resources. Accelerated changes in the vegetation cover within the biogeographical units, added to the increase of agricultural zones and cattle ranching, become determinant factors for the survival of the populations. In addition, it is urgent the design of strategies that involve the local communities and the adequate local and regional authorities. The right stakeholders should start by getting to know the problematic around the high Andean amphibians and butterflies; so, they can take part in the potential solution towards the conservation of the fauna they should learn how to appreciate and value. All of the above are reasons why it is important to assess the diversity of amphibians and butterflies at elevations higher than 2500 m a.s.l. (Fig. 3a, b), as a model to identify priority areas for conservation in the high Andean region.

CONCLUSIONS

Main bioclimatic predictors for the potential richness of most amphibians' species are related to the mean annual temperature (BIO 1) and precipitation (BIO 19). For the species of butterflies, on the other hand, the main predictors of their potential richness patterns were related to isothermality (BIO 3), understood as the level of variation between diurnal and nocturnal temperatures, in relation to the range of annual temperature. Similarly, the minimum temperature of the coldest months (BIO 6), the maximum temperature of the warmest months (BIO 5) and the precipitation (BIO 19), had important contributions to the models.

The ESR showed distribution patterns that pointed out a spatial interconnection between the different biogeographical units (Almorzadero, Santurbán, and Tamá), for both frogs and diurnal butterflies (superfamily Papilionoidea) (Fig. 2a, b). The highest richness of species of amphibians was concentrated in the altitudinal range from 1500m to 3000 m a.s.l., which corresponds to the vegetation covers of Andean forest and High Andean forest; whereas, for butterflies, the highest richness was found above 3000 m a.s.l., mainly in the paramo.

Our results demonstrate the importance of maintaining the ecological corridors between the biogeographical units, which harbor important centers of diversity and endemism. An example is the frog genus *Pristimantis*; the majority of its species occur at altitudes between 2000 and 3500 m a.s.l., because this range offers the adequate habitats that contribute towards the distribution of these organisms. Similarly, the butterflies' subtribe Pronophilina exhibit high diversity in the high Andean mountains.

ACKNOWLEDGEMENTS

This work would not have been possible without the financial support of COLCIENCIAS through its Convocatoria-Bio 659-2014 (Project code 1121-659-44242, contract 553 of 2014). Special thanks to Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia,

and the project "Delimitación de Páramos." The authors thank the personnel at the Vicerrectoría de Investigaciones from the Universidad de Pamplona for their logistic support. Mónica Martínez helped with fieldwork and the reviewers for their valuable comments that helped to improve this manuscript significantly.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

REFERENCES

- Acevedo AA, Armesto O, Franco R, Silva K, Gallardo A. *Gastrotheca helenae*. Catálogo de Anfibios y Reptiles de Colombia. 2014;2(1):11-15.
- Acevedo AA, Silva KL, Franco R, Lizcano DJ. Distribución, historia natural y conservación de una rana marsupial poco conocida, *Gastrotheca helenae* (Anura: Hemiphractidae), en el Parque Natural Nacional Tamá. Bol Cien Mus His Nat. 2011;15:68-74.
- Acevedo AA, Franco R, Carrero D. Diversity of Andean amphibians of the Tamá National Natural Park in Colombia: a survey for the presence of *Batrachochytrium dendrobatidis*. Anim Biodivers Conserv. 2016a;39(1):1-10.
- Acevedo AA, Martínez M, Armesto O, Solano L, Silva K, Lizcano D. Detection of *Batrachochytrium dendrobatidis* in Amphibians from Northeastern Colombia. Herpetol Rev. 2016b;47(2):220-226.
- Acosta AR. 2017. Lista de los Anfibios de Colombia. Referencia en línea V.05.2015.0. Available in: <http://www.batrachia.com>. Cited: 20 Mar 2017.
- Albornoz-Espinell MM, Cáceres C, Acevedo AA. Protected areas assessment for the conservation of threatened amphibians in the Cordillera Oriental of Colombia. Herpetology Notes. 2017;10:685-696.
- Alcock J. Leks and hilltopping in insects. Ann Mag Nat Hist. 1987;21:319-328. Doi:10.1080/00222938700771041
- AmphibiaWeb. 2018. AmphibiaWeb: Information on amphibian biology and conservation. Available in: <https://amphibiaweb.org>. Cited: 22 Apr 2018.
- Andrade-C. MG, Amat G. Estudio regional de las mariposas altoandinas en la cordillera Oriental de Colombia. In: Andrade-C. MG, Amat G, Fernández F, editors. Insectos de Colombia. Bogotá D.C.: Academia Colombiana de Ciencias Exactas, Físicas y Naturales; 1996. p. 149-180.
- Andrade-C. MG. Estado del conocimiento de la biodiversidad en Colombia y sus amenazas. Consideraciones para fortalecer la interacción ciencia-política. Rev Acad Colomb Cienc Exactas Fis Nat. 2011;35(137):491-507.
- Andrade-C. MG, Henao E, Triviño P. Técnicas y Procesamiento para la Recolección, Preservación y Montaje de Mariposas en Estudios de Biodiversidad y Conservación (Lepidoptera: Hesperioidea-Papilionoidea). Rev Acad Colomb Cienc Exactas Fis Nat. 2013;37(144):311-325. Doi:10.18257/raccefyn.12

- Armenteras D, Gast F, Villareal H. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biol Conserv.* 2003;113:245-256. Doi:10.1016/S0006-3207(02)00359-2
- Armesto LO, Señaris JC. Anuros del norte de los Andes: riqueza de especies y estado de conservación. *Pap. Avulsos Zool.* 2017;57: 491-526. Doi:10.11606/0031-1049.2017.57.39
- Bernal MH, Lynch JD. Review and analysis of altitudinal distribution of the Andean anurans in Colombia. *Zootaxa.* 2008;1826:1-25. Doi:10.11646/zootaxa.1826.1.1
- Brown JL. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol.* 2014;5:694-700. Doi:10.1111/2041-210X.12200
- Carrero D, Sanchez LR, Tobar-López D. Diversidad y distribución de mariposas diurnas en un gradiente altitudinal en la región nor-oriental Andina de Colombia. *Bol Cient Mus His Nat.* 2013;17(1):168-188.
- Crump ML, Scott Jr NJ. Visual encounter surveys. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS, editors. *Measuring and Monitoring Biological Diversity, Standard Methods for Amphibians*, Washington D.C.: Smithsonian Institution Press; 1994. p. 84-92.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. *Divers Distrib.* 2011;17:43-57. Doi:10.1111/j.1472-4642.2010.00725.x.
- ESRI. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute; 2011.
- Figuerola J, Stucchi M, Rojas-Vera Pinto R. Modelación de la distribución del oso andino *Tremarctos ornatus* en el bosque seco del Marañón (Perú). *Rev Mex Biodivers.* 2016;87:230-238. Doi:10.1016/j.rmb.2016.01.008
- Ferrier S. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here?. *Syst Biol.* 2002;51:331-363. Doi:10.1080/10635150252899806
- Gámez R. Guía para la elaboración de mapas de distribución potencial. 1 ed. Veracruz: Universidad de Veracruzana; 2011. p. 38.
- García-Perez JF, Ospina-López LA, Villa-Navarro FA, Reinoso-Flórez G. Diversidad y distribución de mariposas Satyrinae (Lepidoptera: Nymphalidae) en la cuenca del río Coello, Colombia. *Rev Biol Trop.* 2007;55:645-653. Doi:10.15517/rbt.v55i2.6039
- Gaviria-Ortiz F, Henao-Bañol E. Diversidad de mariposas diurnas (Hesperioidea y Papilionoidea) del Parque Natural Regional El Vínculo (Buga-Valle del Cauca). *Bol Cient Mus His Nat.* 2011;15(1):115-133.
- Heinicke MP, Duellman WE, Hedges SB. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proc Natl Acad Sci USA.* 2007;104:10092-10097. Doi:10.1073/pnas.0611051104
- Herzog SK, Kattan GH. Patterns of diversity and endemism in the birds of the tropical andes. In: Herzog SK, Martínez R, Jørgensen P.M, Tiessen H, editors. *Climate change and biodiversity in the tropical Andes*. Paris: McArthur Foundation, Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE); 2011. p. 245-259.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol.* 2005;25:1965-1978. Doi:10.1002/joc.1276
- IDEAM. Leyenda Nacional de Coberturas de la Tierra. Metodología CORINE Land Cover adaptada para Colombia Escala 1:100.000. Instituto de Hidrología, Meteorología y Estudios Ambientales. Bogotá, D. C.; 2010. p. 72.
- La Marca E. Ecología de anfibios en dos ambientes contrastantes (selva nublada y páramo) de la Cordillera de Mérida, Venezuela. In: Universidad de Los Andes, Instituto de Geografía y Conservación de Recursos Renovables, editors. *Anuario de Investigación*. Mérida: Instituto de Geografía, Universidad de Los Andes; 1994. p. 31-37.
- La Marca E. *Dendropsophus meridensis*. The IUCN Red List of Threatened Species 2004: e.T55555A11331704. Available in: <http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T55555A11331704.en>. Cited: 30 Nov 2016.
- Lamas G, Vilorio A, Pyrcz T. Subtribe Pronophilina. In: Lamas G, editor. *Atlas of Neotropical Lepidoptera, checklist: Part: 4A, Hesperioidea-Papilionoidea*. Gainesville: Association for Tropical Lepidoptera; 2004. p. 206-215.
- Levinsky I, Skov F, Svenning J, Rahbek C. Potential impacts of climate change on the distributions and diversity patterns of European mammals. *Biodivers Conserv.* 2007;16:3803-3816. Doi:10.1007/s10531-007-9181-7
- Lobo JM, Jiménez-Valverde A, Hortal J. The uncertain nature of absences and their importance in species distribution modelling. *Ecography.* 2010;33:103-114. Doi:10.1111/j.1600-0587.2009.06039.x
- Lynch JD. La riqueza de la fauna anfibia de los Andes colombianos. *Innovación y Ciencia.* 1998;7(4):46-51.
- Lynch JD, Suárez-Mayorga MA. Análisis biogeográfico de los anfibios paramunos. *Caldasia.* 2002;24(2):471-480.
- Mahecha-Jiménez OJ, Dumar-Rodríguez JC, Pyrcz TW. Efecto de la fragmentación del hábitat sobre las comunidades de Lepidoptera de la tribu Pronophilini a lo largo de un gradiente altitudinal en un bosque andino en Bogotá (Colombia) (Lepidoptera: Nymphalidae, Satyrina). *SHILAP Soc Hispano Luso Am Lepid.* 2011;39(153):117-126.
- Manel S, Williams HC, Ormerod SJ. Evaluating presence-absence models in ecology: the need to account for prevalence. *J Appl Ecol.* 2001;38:921-931. Doi:10.1046/j.1365-2664.2001.00647.x

- Marín MA, Giraldo C, Marín A, Álvarez CF, Pyrcz TW. Differences in butterfly (Nymphalidae) diversity between hillsides and hilltop forest patches in the northern Andes. *Stud Neotrop Fauna Environ.* 2015;50(3):194-203. Doi: 10.1080/01650521.2015.1099379
- Meza-Joya FL, Torres M. Spatial diversity patterns of *Pristimantis* frogs in the Tropical Andes. *Ecol Evol.* 2016;6:1901-1913. Doi:10.1002/ece3.1968
- Morales M, Otero J, Van der Hammen T, Torres A, Cadena C, Pedraza C, *et al.* Atlas de páramos de Colombia. 1 ed. Bogotá D.C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; 2007. p. 208.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J. Biodiversity hotspots for conservation priorities. *Nature.* 2000;403:853-858. Doi:10.1038/35002501
- Obregón R, Fernandez J, Jordano D. Effects of climate change on three species of Cupido (Lepidoptera, Lycaenidae) with different biogeographic distribution in Andalusia, southern Spain. *Anim Biodivers Conserv.* 2016;39(1):115-128.
- Ortíz-Yusty C, Restrepo A, Páez VP. Distribución potencial del *Podocnemis lewyana* (Reptilia: Podocnemididae) y su posible fluctuación bajo escenarios de cambio climática global. *Acta biol. Colomb.* 2014;19(3):471-481.
- Pearson RG, Dawson TP. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?. *Glob Ecol Biogeogr.* 2003;12(5):361-371. Doi:10.1046/j.1466-822X.2003.00042.x
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr.* 2007;34:102-117. Doi:10.1111/j.1365-2699.2006.01594.x
- Pennington RT, Lavin M, Särkinen T, Lewis GP, Klitgaard BB, Hughes CE. Contrasting plant diversification histories within the Andean biodiversity hotspot. *Proc Natl Acad Sci USA.* 2010;107:13783-13787. Doi:10.1073/pnas.1001317107
- Pe'er G, Saltz D, Thulke HH, Motro U. Response to topography in a hilltopping butterfly and implications for modelling nonrandom dispersal. *Anim Behav.* 2004;68:825-839. Doi:10.1016/j.anbehav.2004.02.006
- Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. *Ecol Modell.* 2006;190:231-259. Doi:10.1016/j.ecolmodel.2005.03.026
- Prieto C, Dahners HW. Eumaeini butterflies (Lepidoptera: Lycaenidae) from San Antonio hill: Richness dynamic and hilltopping behaviour. *Rev Colomb Entomol.* 2006;32:179-190.
- Pyrcz TW, Rodríguez G. Mariposas de la tribu Pronophilini en La Cordillera Occidental delos Andes Colombia (Lepidoptera: Nymphalidae, Satyrinae). *SHILAP Soc Hispano Luso Am Lepid.* 2007;35(140):455-489. Doi:10.1590/S1519-566X2009000600003
- Pyrcz TW, Vilorio AL. Erebiine and pronophiline butterflies of the Serranía del Tamá, Venezuela-Colombia border (Lepidoptera: Nymphalidae: Satyrinae). *Trop Lepid Res.* 2007;15(2):18-52.
- Pyrcz TW, Wojtusiak J, Garlacz R. Diversity and distribution patterns of Pronophilina Butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in North-Western Ecuador. *Neotrop Entomol.* 2009;38(6):716-726.
- Pyrcz TW, Lorenc J, Knoop DP. New species of *Euphaedra* Hübner of the ceres group from southwestern Nigeria – with new evidence from female genital morphology (Lepidoptera: Nymphalidae: Limenitidinae). *Genus.* 2011;22(4):621-638.
- Rangel-Ch. JO, editor. Colombia Diversidad Biótica III. La región de vida paramuna. Bogotá D.C.: Instituto de Ciencias Naturales – Instituto Alexander von Humboldt; 2000. p. 902.
- Rangel-Ch. JO. La biodiversidad de Colombia: significado y distribución regional. *Rev Acad Colomb Cienc Exact Fis Nat.* 2015;39(151):176-200. Doi:10.18257/raccefyn.136
- Ríos-Málaver C. Riqueza de especies de mariposas (Hesperioidea and Papilionoidea) de la quebrada “El Águila” Cordillera Central (Manizales, Colombia). *Bol Cient Mus His Nat.* 2007;11:272-291
- Rodríguez N, Armenteras D, Morales M, Romero M. Ecosistemas de los Andes colombianos. 2 ed. Bogotá D.C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; 2006. p. 154.
- Romo H, Sanabria P, García-Barros E. Predicción de los impactos del cambio climático en la distribución sobre las especies de Lepidoptera. El caso del género *Boloria* Moore, 1900 en la Península Ibérica (Lepidoptera: Nymphalidae). *SHILAP Soc Hispano Luso Am Lepid.* 2013;41(162):267-286.
- Shields O. Hilltopping: an ecological study of summit congregation behavior of butterflies on a southern California hill. *J Res Lepid.* 1967;6:69-178.
- Soberón J, Peterson AT. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics.* 2005;2:1-10. Doi:10.17161/bi.v2i0.4
- Terborgh J. Diversity and the Tropical Rain Forest. 1 ed. Freeman, New York: Scientific American Library Series; 1992. p. 111.
- Tognelli MF, Roig-Juñent SA, Marvaldi AE, Flores GE, Lobo JM. An evaluation of methods for modelling distribution of Patagonian insects. *Rev Chil Hist Nat.* 2009;82:347-360. Doi:10.4067/S0716-078X2009000300003
- Van Swaay C, Regan E, Ling M, Bozhinovska E, Fernandez M, Marini-Filho OJ, *et al.* Guidelines for Standardised

- Global Butterfly Monitoring. 1 ed. Leipzig: Group on Earth Observations Biodiversity Observation Network; 2015. p. 32.
- Villareal H, Álvarez M, Córdoba S, Escobar F, Fagua G, Gast F, *et al.* Manual de métodos para el desarrollo de inventarios de biodiversidad. Programa de Inventarios de Biodiversidad. 1 ed. Bogotá D.C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; 2004. p. 236.
- Viloria AL, Pyrcz TW, Orellana A. A survey of the Neotropical montane butterflies of the subtribe Pronophilina (Lepidoptera, Nymphalidae) in the Venezuelan Cordillera de la Costa. *Zootaxa*. 2010;2622:1-41.
- Wang IJ, Crawford AJ, Bermingham E. Phylogeography of the pygmy rain frog (*Pristimantis ridens*) across the lowland wet forests of isthmian Central America. *Mol Phylogenet Evol*. 2008;47:992-1004. Doi:10.1016/j.ympev.2008.02.021
- Ward DF. Modelling the potential geographic distribution of invasive ant species in New Zealand. *Biol Invasions*. 2007;9:723-735. Doi:10.1007/s10530-006-9072-y