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Colegio de Posgrados

**Biogeographical and ecological patterns of allometric trends variations
in Ecuadorian *Stenocercus* (Iguanidae: Tropidurinae) species**

Tesis

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**Biogeographical and ecological patterns of allometric trends variations
in Ecuadorian *Stenocercus* (Iguanidae: Tropidurinae) species**

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RESUMEN

Por más de un siglo estudios han demostrado la relación entre las variables medioambientales y la morfología de las especies. Se han planteado patrones biogeográficos y macroevolutivos con varios grupos de fauna alrededor del mundo, obteniendo diferentes resultados para especies endotérmicas o ectotérmicas. Escogimos como grupo modelo al género de lagartijas *Stenocercus*, para explorar este tipo de patrones en especies ectotérmicas en la región neotropical. Exploramos variaciones alométricas intraespecíficas y analizamos datos morfológicos lineales de doce especies de Ecuador a lo largo de su distribución altitudinal y latitudinal. Además, analizamos la relación de las variaciones morfológicas con variables bioclimáticas. Encontramos que las especies de *Stenocercus* distribuidas en altitudes mayores tienen patas delanteras y traseras más cortas, mientras que las especies distribuidas en altitudes más bajas tienen patas más largas. No encontramos una relación significativa entre el SVL con la distribución altitudinal o latitudinal, obtuvimos el mismo resultado con la longitud de la cabeza. La altitud y estacionalidad de la precipitación (Bio15) son las variables explicativas de mayor importancia para nuestros resultados. Finalmente, discutimos sobre las potenciales razones para entender estos patrones biogeográficos y sugerimos continuar el tipo de estudios considerando otras variables medioambientales a diferente escala.

Palabras clave: Biogeografía, alometría, especies ectotérmicas, morfología, Squamata, Sauria.

ABSTRACT

For more than a century, studies have shown the relationship between environmental variables and species morphology. Biogeographic patterns have been raised with several fauna groups around the world, obtaining different results for endothermic and ectothermic species. We chose *Stenocercus* genus lizards as a model group to explore this kind of pattern in ectothermic species in the neotropical region. We explored intraspecific allometric variations and analyzed linear morphological data of twelve species from Ecuador through their elevational and latitudinal distribution. Besides, we analyzed the relationship between morphological variations with bioclimatic variables. We found that *Stenocercus* species distributed in higher elevations have shorter forelimbs and hindlimbs, while species distributed in lower elevations have longer limbs. We did not find a significative relationship between SVL with elevational or latitudinal distribution, we found the same result for head length. Elevation and precipitation seasonality (Bio15) are the most important explicative variables for our results. Finally, we discussed the potential reasons to understand these biogeographic patterns and suggested continuing this kind of study considering other environmental variables on different scale.

Key words: Biogeography, allometry, ectothermic species, morphology, Squamata, Sauria.

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Introduction

For more than a century, studies have demonstrated the relationship between environmental and ecological variables with body size and morphological traits, which are related to physiology, reproduction, sexual selection, fitness, and ecological aspects of species (Ma et al. 2019; Blanckenhorn 2000; Allen 1877; Bergmann 1847). By studying these relationships, biogeographic and macroevolutionary patterns have been found between species or between populations of one species. To understand these patterns in intra or interspecific studies it is necessary to consider all possible variables involved, one tool that is useful to understand their complexity is allometric analysis. Allometry refers to the relationships between body size and other organismal traits and could help to understand the relationships of species morphology with ecological variables and implications of evolutionary processes (Pérez-Quintero et al. 2019; Shingleton 2010; Cooper & Purvis 2009). There are three types of allometry, static, evolutionary, and ontogenetic; the first one refers to analyzing traits covariation within the same species in a specific ontogenetic stage; the second one is similar but analyzing interspecific traits covariation in lineages with the same ancestor; and the last one analyzes traits covariation considering different ontogenetic stages of growth (Klingenberg & Zimmerman 1992; Cock 1966; Gould 1966).

On the other hand, environmental variables such those related to climate have an important role in the habitat structure and are directly related to physiology, morphology, reproduction, and other aspects of ectotherm species like reptiles (Jaffe et al. 2016; Grizante et al. 2012; Brandt & Navas et al. 2011; Oufiero et al. 2011). Analyzing the climate variables and the ecosystems in the distribution of ectotherm species could provide valuable information to understand morphological patterns and their variations.

Stenocercus is a genus of lizards from the Iguanidae family, with 80 species in South America (Uetz 2022). Within Ecuador, 17 species of the genus are distributed in the continental territory from lowlands to highlands on both sides of the Andes Mountain range (Torres-Carvajal et al. 2022). Phylogenetic and morphological studies have established this clade as a monophyletic group well supported (Torres-Carvajal 2007a; Torres-Carvajal 2007b). Additionally, due to its wide altitudinal and latitudinal distribution, including ecosystem heterogeneity, and well-known richness, *Stenocercus* is considered an ecologically and morphologically diversified taxon (Brandt & Navas 2011). Hence, it could be considered a model group to explore allometry and biogeographical patterns.

Several biogeographic and macroecological studies have been performed with South American lizard species (Edwards et al. 2022; Velasco et al. 2020; Valdecantos et al. 2019; Breitman et al. 2015; Brandt & Navas 2011). Despite the taxonomy and phylogeny of the genus have been well studied and some ecological data have been published, there are no studies that explore biogeographic or ecogeographic patterns (Ramírez-Jaramillo et al. 2015; Pérez et al. 2012; Pérez & Morales 2011; Torres-Carvajal 2007a; Torres-Carvajal 2007b; Fritts 1974). Performing studies about biogeographic patterns is critical to understand the relationship between the species and the environment. To our knowledge only one study deal with the biogeography of *Stenocercus*, which is focused on the spatial and temporal diversification of the genus (Teixeira et al. 2016).

Biogeographic patterns data is a basis to further studies analyzing environmental, ecological, and biological variables to understand their impacts on the survival of the species. Mainly in ectotherms species such as *Stenocercus* lizards which directly depend on environmental temperature to have normal development in biological processes such as thermoregulation, reproduction, feeding, etc. Carrying out this kind of study gives us

tools to work in the conservation of species, considering that the planet is being hardly affected by climate change and global warming. In this context, the aims of this study are:

1) To establish the relationship between morphological traits with elevation and latitude within Ecuadorian *Stenocercus* species; 2) To explore allometric patterns variations (i.e., allometric slope-related) between species of *Stenocercus* genus present in Ecuador, through elevation and latitudinal range distribution; and 3) To identify biogeographic patterns and the relationships between morphological variations of *Stenocercus* species with environmental variables and the ecosystems they inhabit in Ecuador.

In this context, the aims of this study seek to establish the relationship between morphological traits with elevation and latitude within Ecuadorian *Stenocercus* species; to explore allometric patterns variations; and to identify biogeographic patterns and the relationships between morphological variations with environmental variables and the ecosystems they inhabit in Ecuador.

Methods

Morphological data

We used adult males to perform analysis of evolutionary and static allometry. To avoid effects of sexual dimorphism and bias we excluded females and juveniles. We took measurements data from specimens preserved and deposited in 11 scientific collections. From September to November 2022, we obtained morphological data from Ecuadorian museums: Museo de Zoología, Universidad San Francisco de Quito, Ecuador (ZSFQ); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); División de Herpetología, Instituto Nacional de Biodiversidad, Quito, Ecuador (DHMECN); Museo de Zoología, Universidad Técnica Particular de Loja, Ecuador (MUTPL-R); and Museo de Zoología, Universidad del Azuay, Ecuador (MZUA-RE). We complemented the database with morphological data obtained from national and

international scientific collections cited in Torres-Carvajal (2007a; 2007b) (complementary database).

We used data from 182 males of 12 species of *Stenocercus* for this study, the specimens' number per species varies depending on the availability in scientific collections. We ensured that the twelve species can represent the genus, for having a wide elevational and latitudinal distribution and for occupying a wide variety of ecosystems. We took standard measurements following Torres-Carvajal (2007a) and morphological variation studies (Pérez-Quintero et al. 2019; Breitman et al. 2015; Bula et al. 2014). We did analyze with four measurements: Snout vent length (SVL) from the tip of the snout to cloaca; Head length (HL) from the tip of the snout to the posterior surface of the quadrate bone; Forelimb length (FLL) from the insertion of the arm to the tip of the third finger; and Hindlimb length (HLL) from the insertion of the leg to the tip of the fourth toe. These measurements have provided useful information in several studies with similar objectives (Schools et al. 2022; Pérez-Quintero et al. 2019; Valdecantos et al. 2019; Melville et al. 2005; Kohlsdorf et al. 2001). We took measurements with digital calipers with a precision of 0.1 mm. Measurements of both database initial and complementary were taken independently by one only person. To reduce the error range in taking measures, we took three times each measure, then we obtained the mean and used that value.

Statistical analysis

Biogeographical and allometric analysis

To explore data and detect outliers, we made boxplots separated by species, and for contrast data normality, we applied Shapiro-Wilk test (Shapiro & Wilk 1965). The normality test was applied to decide what kind of statistic (parametric, non-parametric) is the most adequate to analyze our data. For reducing the effect of body size on other traits,

and to obtain an approximation of the independent measure of the trait, we standardized them, dividing each character over SVL, which represents body size (Mosimann 1970). We performed General Linear Models (GLMs) through a regression by Generalized Least Square regression (GLS) to explore if there is intraspecific allometry (Kantar 2015; Rencher & Schaalje 2008). We used each trait (HL, FLL, HLL) as the response variable (Y) and SVL values as the explicative variable (X) for twelve species, all values were previously log-transformed (ln). We extract values slope from each linear model performed.

We extracted the minimum and maximum values, calculated the mean and mode of elevation and latitude for each species, and from standardized values of morphological data, we calculated the mean. To determine if there is a relationship between morphological measures with elevation and latitude, we performed linear models by Phylogenetic Generalized Least Square (PGLS). We log-transformed (ln) the values and performed several models for each trait, establishing the trait as the response variable (Y) and as the explicative variable (X) the elevation or latitude. To explore all options, we performed independent linear regressions using mean, mode, minimum, and maximum values of elevation and latitude. Finally, we add intraspecific allometric slope values to PGLS models to perform interaction and additive models to understand if it is a factor that interacts with biogeographic patterns.

Environmental analysis

We compiled all available records of *Stenocercus* species from measured specimens for analysis, scientific publications, and digital repositories (611 records). We ensured that each record compiled had museum code to avoid wrong information. We verified the information based on the updated distribution of the species and eliminated wrong records (Torres-Carvajal et al. 2022, Uetz et al. 2022). We made a minimum convex polygon for

each species, extracting unsuitable areas based on mainly altitudinal distribution. With those polygons, we extracted information from the ecosystems of Ecuador (Ministerio del Ambiente 2013) using Arcgis Pro (ESRI s.f.) to describe the type of ecosystems present in the distributional range of Ecuadorian *Stenocercus* and relate them descriptively with their morphology. We unified the most similar ecosystems into twelve categories to reduce redundancy in the results.

Additionally, we extracted values of pixels (1 km²) where records of each species are located from 19 bioclimatic variables (Bioclim) downloaded from Worldclim (Fick & Hijmans 2017). Those values were log-transformed (ln) and through correlation analysis of Pearson, we selected the variables that are not highly correlated (> 0.8) to use in the following analysis. We performed a correspondence analysis, for which all values need to be on the same scale, hence, we log-transformed bioclimatic variables and elevation values, and used their means (Greenacre 2010).

In this analysis interact bioclimatic variables, elevation, and species to determine how related they are to each other and the contribution of each variable to that pattern. All the statistical analyzes were performed in R software, using Tidyverse, nmle, and factoextra packages (Kassambara & Mundt 2017; Pinheiro et al. 2017; Wickham 2019; R Core Team 2020).

Results

Morphological data

After reviewing all the specimens available in the scientific collections visited, we selected 182 adult males and took the four measurements mentioned above from them. The analyzes were made with twelve species (records number): *Stenocercus angel* (17), *S. angulifer* (8), *S. cadlei* (9), *S. carrioni* (14), *S. chota* (20), *S. festae* (18), *S. guentheri* (18), *S. humeralis* (15), *S. iridescens* (20), *S. ornatus* (16), *S. puyango* (13), *S. rhodomelas*

(14). The distribution of the data of the four morphological measurements is normal, which was proved with Shapiro-Wilk test ($p\text{-value} > 0.05$) (Figure 1).

Intraspecific allometry

Linear models performed to analyze intraspecific allometry show a significative relationship between SVL and other morphological traits (HL, FLL, HLL). Models of twelve *Stenocercus* species present negative slope values, which means that all species have negative allometry. (Appendix II).

Biogeographical and allometric analysis

Based on the coefficient values of linear regressions (Table 1), there is no statistically significant relationship between SVL with elevation and the latitudinal distribution of species. The same result was obtained for HL (Fig. 2). On the other hand, we found a statistically significant relationship between limbs length with elevation. Species with larger limbs are distributed in lower elevations, while species with shorter limbs are distributed in higher elevations (Figs. 3, 4). The relationship between forelimb lengths and elevation is statistically significant ($p\text{-value} < 0.05$), using mean, min, and max values of elevation (Fig. 3). Only the model performed with the mode of elevation does not meet that value (Table 1).

Three groups can be distinguished analyzing the linear models' graphs, group A formed by *S. angel*, *S. cadlei*, *S. festae*, and *S. guentheri*, which are distributed in Azuay, Bolívar, Cañar, Carchi, Cotopaxi, El Oro, Imbabura, Loja, Tungurahua, Chimborazo, and Pichincha provinces in Ecuador, from 1050 to 4051 m a.s.l ($\bar{x} = 2942$ m a.s.l) following records used for the regression; group B formed by *S. carrioni*, *S. chota*, *S. humeralis*, *S. ornatus*, and *S. rhodomelas* are distributed in Azuay, Carchi, El Oro, Imbabura, Loja, Pichincha, and Zamora Chinchipe provinces in Ecuador, from 1130 to 2588 m a.s.l. ($\bar{x} =$

1845 m a.s.l.); and group C formed by *Stenocercus iridescens*, *S. puyango*, and *S. angulifer*, which are distributed in Cañar, Cotopaxi, Chimborazo, El Oro, Esmeraldas, Guayas, Imbabura, Loja, Los Ríos, Manabí, Morona Santiago, Pastaza, Pichincha, Tungurahua and Santa Elena provinces in Ecuador, from 0 to 1447 m a.s.l. ($\bar{x} = 406$ m a.s.l.). For easier visual reading we made Figure 5 where each group is distinguished.

Regarding the latitude, following slope and coefficient values there is not a significant relationship between hindlimb length and this variable. If we consider linear models with the mode and max values, there is a significant relationship with forelimb length (Table 1). Which means that species distributed in latitudes farthest from parallel zero have larger forelimbs than species distributed near parallel zero (Fig. 3). To consider whether elevation affects the relationship between forelimb length and latitude, we repeated the linear model with these two variables but added elevation as an interaction factor. The coefficient values of this model (F-value = 3.0026; p-value = 0.1214) confirmed that the elevation does not infer in this relationship, hence, latitude and forelimb length have a significant relationship independently of elevation.

Finally, the results of interaction and additive models show that intraspecific allometric slopes were not identified as interaction factors to biogeographic patterns between elevation/latitude and traits, and neither contributed to the model (Appendix IV).

Environmental analysis

We selected the more representative ecosystems from minimum convex polygon made for each species and obtained percentages of each one. Some ecosystems were not considered because the percentage was not relevant to the analysis, hence, in no case reach 100%. The highest percentages correspond to Intervention, this item does not represent any native ecosystem because that area is occupied by anthropic activities or structures. We ordered species on the Table 2, considering the same groups mentioned in

the Figure 5. Hence, in the group A the second more representative ecosystem is Grassland of Paramo, followed by Evergreen montane forest, except for *S. festae*; in the group B species occupy wider variety of ecosystems with different environmental conditions as Grassland of Paramo and Desert shrubland; species of the group C occupy drier ecosystems as semi-deciduous or deciduous forest, except *S. angulifer* that occupies evergreen forests (Table 2).

We selected the eight bioclimatic variables that are not highly correlated with each other and performed correspondence analysis (Figure 6). Variables with the highest contribution to the species distribution on the graph are elevation and Bio15 (Precipitation Seasonality) (Appendix V).

Discussion

To analyze biogeography, ecogeography, or macroevolution on a big scale is difficult due to the availability of morphological data of taxonomic groups with a large number of species, but studies with a part of those taxa can help to infer the results for the whole group. *Stenocercus* genus in Ecuador is distributed along the Los Andes Mountain Range eastern and western foothills and lowlands, occupying a wide elevational range and diversity of ecosystems (Torres-Carvajal et al. 2022; Uetz 2022). Hence, our results contribute information to understand the variation of biogeographic and macroevolutionary patterns in neotropical lizards through the diversified taxon *Stenocercus* (Brandt & Navas 2011).

The elevation is correlated with temperature, thus in higher elevations the temperature decrease. Similarly happens with latitude, in higher latitudes the temperature decrease. In this context, biogeographic studies show the relationship between morphology and distribution. Most of these studies with endotherm species describe biogeographic patterns that could be compared with the biogeographic rules proposed by Bergman and

Allen (Allen 1877; Bergmann 1847). But studies with ectotherm species have diversified results (Ma et al. 2019; Rivas et al. 2018; Shelomi & Zeuss 2017; Alho et al. 2010; Olalla-Tárraga et al. 2006). Particularly in lizards and snakes, the body increases with temperature and decreases the size with latitude (Ashton & Feldman 2003). Our results do not show a significant relationship between body size (SVL) and elevation, consequently with temperature. It means that there is no variation in body size based on the altitudinal distribution of the Ecuadorian *Stenocercus* species. This pattern probably is the same if we include all *Stenocercus* species because Ecuadorian species are distributed from 0 to 4800 m a.s.l. and other species occupy a similar elevational range in South America (Texeira et al. 2016; Torres-Carvajal 2007a). The relationship with latitude was not significant either. However, this pattern could vary if we include the *Stenocercus* species distributed farther from zero parallel (e.g. *S. pectinatus*) because the size of Ecuador does not have a wide range of latitudinal distribution (Uetz et al. 2022; Olalla-Tárraga et al. 2006; Ashton & Feldman 2003). This finding makes sense in ectotherms organisms because having a smaller body size in colder environments is an advantage, following the principle that the larger the body, the slower the rate of heating for the proper functioning of the body (Ashton & Feldman 2003). Pincheira-Donoso et al. (2007) found similar results to ours with a group of tropidurid lizards of the genus *Liolaemus*, which is a relatively closer clade to *Stenocercus* (Schulte et al. 2003). There was also no significant relationship between head length and elevation and latitudinal distribution. This trait variation is generally related to ecological aspects such as diet, bite force, or evolutive processes such as sexual selection in lizards but not directly to environmental variables like elevation or temperature (Huyghe et al. 2005; Verwajen et al. 2002). If we include female head data in future studies, probably we find variations related to sexual dimorphism and sexual selection. Additionally, studies about the head

shape through geometric morphology could provide more information to detect morphological variations on the head and to understand their causes.

On the other hand, our results regarding limbs are similar to Allen's rule, which states that species distributed at colder environments (higher elevations or latitudes) have shorter appendages (Allen 1877). By contrast, in linear models performed with limbs against latitude, only forelimbs show a significant relation but show the converse to Allen's rule. However, this result is not well supported because statistical significance changes if we use the mean of latitude instead of the mode value (see Table 1). This last pattern probably varies if we consider species distributed in higher latitudes because Ecuadorian territory cannot provide a wide range of latitudes. A variation in limbs length could be related to many environmental factors, but considering linear models and correspondence analysis the elevation is one of the most important explicative variables to our results. The elevation variation is related to changes in the vegetation composition, temperatures, precipitation rates, etc. (Ministerio del Ambiente 2013). Following the same principle that the larger the body, the slower the rate of heating, having shorter limbs in colder environments is an advantage because the total body size is smaller too, and the individual can warm up faster (Ashton & Feldman 2003).

Several studies have demonstrated the relationship between limbs length with habitat and microhabitat (Kohlsdorf et al. 2001; Losos 1999, 1992; Losos & Irschick 1996; Williams 1972, 1983). In our study, the analysis of ecosystems where *Stenocercus* inhabit gives us a general idea about their habitats (Ministerio del Ambiente 2013). However, there are no patterns to infer if a type of ecosystem is directly related to limb length. Besides, there is no available detailed information about their habitats as the type of substrate, percentage of vegetation cover, and local environmental data, among other factors. Based on scarce available ecological information of *Stenocercus* genus, their species have similar habits

and prefer exclusively terrestrial habitats with low shrubs, agave plants, rocks, trunks, etc. (Torres-Carvajal 2007a; Fritts 1974). Excepting *S. varius* and *S. guentheri* that have been recorded in arboreal perch (Ramirez-Jaramillo et al. 2015; Torres-Carvajal 2007a). Hence, we cannot infer that variation in limbs length could be modified by habitat preferences because there is no evidence of habitat specialization. Jaksic et al. (1980) demonstrated that in a group of *Liolaemus* genus, the proportion of body size and appendages do not vary in relation to microhabitat. However, following the ecosystem analysis, 92% of the species inhabit mainly in intervened areas. It could mean that the species have adapted to anthropic areas, or they are occupying remnants of vegetation in those areas. Lower percentages of ecosystems are diverse, evergreen forest, deciduous forest, paramo, shrubland, etc. Therefore, it is necessary to study on a fine scale the development of *Stenocercus* species in their habitats to explore the relationship with limb length.

Lizard limb length is related to their performance in the habitat, thus, species from more open areas have larger limbs than species from habitats with more vegetation (Melville & Swain 2000). Because lizards in open areas are more visible to predators, hence, if those species have no strategies to avoid predation different from scaping, they need larger limbs to have higher sprint speed (Bula et al. 2014; Bonine 1999). Besides, Bula et al. (2014) demonstrated that populations of side-blotched lizards from areas with higher abundance and diversity of predators have larger limbs than individuals in other areas. There is little available data about the predation of *Stenocercus*, so it is necessary to analyze more deeply trophic relationships of the genus to explore if the limb length is related to those factors (Reina 2019; Cadena-Ortiz et al. 2017; Ramirez-Jaramillo et al. 2015).

We highlighted the scarce availability of ecological information about *Stenocercus* species and of other neotropical reptiles. However, our results provide information about biogeographic patterns, and allometry, which is useful to continue studying the ecology not only of *Stenocercus* genus but in ectothermic species of the Neotropical region. Biogeographic patterns are a tool to analyze other variables related to altitude and latitude that could infer morphological and physiological adaptations. It could be useful to evaluate the potential impacts of climate change and global warming on ectothermic species and estimates their vulnerability. The wide altitudinal distribution of some analyzed species and the diversity of ecosystems that they occupy, give us important information to perform intraspecific studies of adaptation. In the same context, the negative allometry that we found in all species could be analyzed more deeply between populations of the same species. Our pioneer findings in an Ecuadorian reptile group are a starting point to continue studies in biogeography, ecogeography, and evolution with neotropical ectothermic species.

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Tables

Table 1.- Coefficient values of linear regressions between morphological traits with elevation and latitude distribution.

Model	Statistic	Std.Error	t-value	p-value
SVL~Elev (mode)	-0.000028	0.00003147	-0.9006	0.389
SVL~Lat (mode)	0.004295	0.01982072	0.21669	0.8328
HL~Elev (mode)	0.0000107	0.000011299	0.95101	0.364
HL~Lat (mode)	0.006052	0.006903307	0.87668	0.4012
HLL~Elev (mode)	-0.00007056	0.0000211	-3.343133	0.0075
HLL~Elev (mean)	-0.00006788	0.00001819	-3.73208	0.0039
HLL~Elev (min)	-0.00007939	0.00002246	-3.534586	0.0054
HLL~Elev (max)	-0.00004643	0.00001664	-2.790659	0.0191
HLL~Lat (mode)	0.0198454	0.01755832	1.130259	0.2847
HLL~Lat (mean)	0.01123058	0.01900178	0.591028	0.5676
HLL~Lat (min)	0.00466929	0.01791998	0.260563	0.7997
HLL~Lat (max)	0.0219385	0.01812731	1.210245	0.254
FLL~Elev (mode)	-0.0000384	0.00001856	-2.070072	0.0653
FLL~Elev (mean)	-0.0000432	0.00001505	-2.869888	0.0167
FLL~Elev (min)	-0.0000468	0.000019307	-2.42485	0.0358
FLL~Elev (max)	-0.00004	0.000009825	-4.076337	0.0022
FLL~Lat (mode)	0.0263752	0.01057481	2.494155	0.0318
FLL~Lat (mean)	0.0234626	0.01182827	1.983606	0.0754
FLL~Lat (min)	0.018894	0.01153159	1.638459	0.1324
FLL~Lat (max)	0.0262099	0.01130717	2.317989	0.0429

Table 2.- Percentages of ecosystems obtained of minimum convex polygon.

Group	Species	Ecosystem	Percentage
A	<i>S. angel</i>	Intervention	64.5%
		Grassland of Paramo	29.5%
		Evergreen montane forest	5.8%
	<i>S. cadlei</i>	Intervention	64.4%
		Grassland of Paramo	30.0%
		Intervention	42.7%
	<i>S. festae</i>	Evergreen montane forest	22.8%
		Grassland of Paramo	19.9%
		Intervention	56.1%
	<i>S. guentheri</i>	Grassland of Paramo	16.1%
		Evergreen montane forest	15.5%
		B	<i>S. carrioni</i>
Seasonal montane evergreen forest	28.5%		
<i>S. chota</i>	Intervention		55.1%

Group	Species	Ecosystem	Percentage
		Evergreen montane forest	16.5%
		Grassland of Paramo	9.8%
		Semi-deciduous forest and shrubland	8.8%
	<i>S. humeralis</i>	Intervention	38.4%
		Semi-deciduous montane forest	30.5%
		Evergreen montane forest	11.8%
		Semi-deciduous shrubland	10.2%
	<i>S. ornatus</i>	Intervention	47.5%
		Semi-deciduous montane forest	13.4%
		Evergreen montane forest	13.2%
		Semi-deciduous shrubland	9.0%
	<i>S. rhodomelas</i>	Intervention	49.7%
		Semi-deciduous shrubland	14.8%
		Desert shrubland	11.1%
		Evergreen montane forest	6.2%
	<i>S. iridescens</i>	Intervention	65.7%
		Seasonal montane evergreen forest	7.9%
		Evergreen montane forest	5.1%
C	<i>S. puyango</i>	Intervention	38.4%
		Deciduous forest of lowlands	18.1%
		Deciduous montane forest	14.5%
		Semi-deciduous montane forest	14.1%
	<i>S. angulifer</i>	Evergreen forest of lowlands	43.8%
		Evergreen montane forest	31.8%
		Intervention	16.7%

Figures

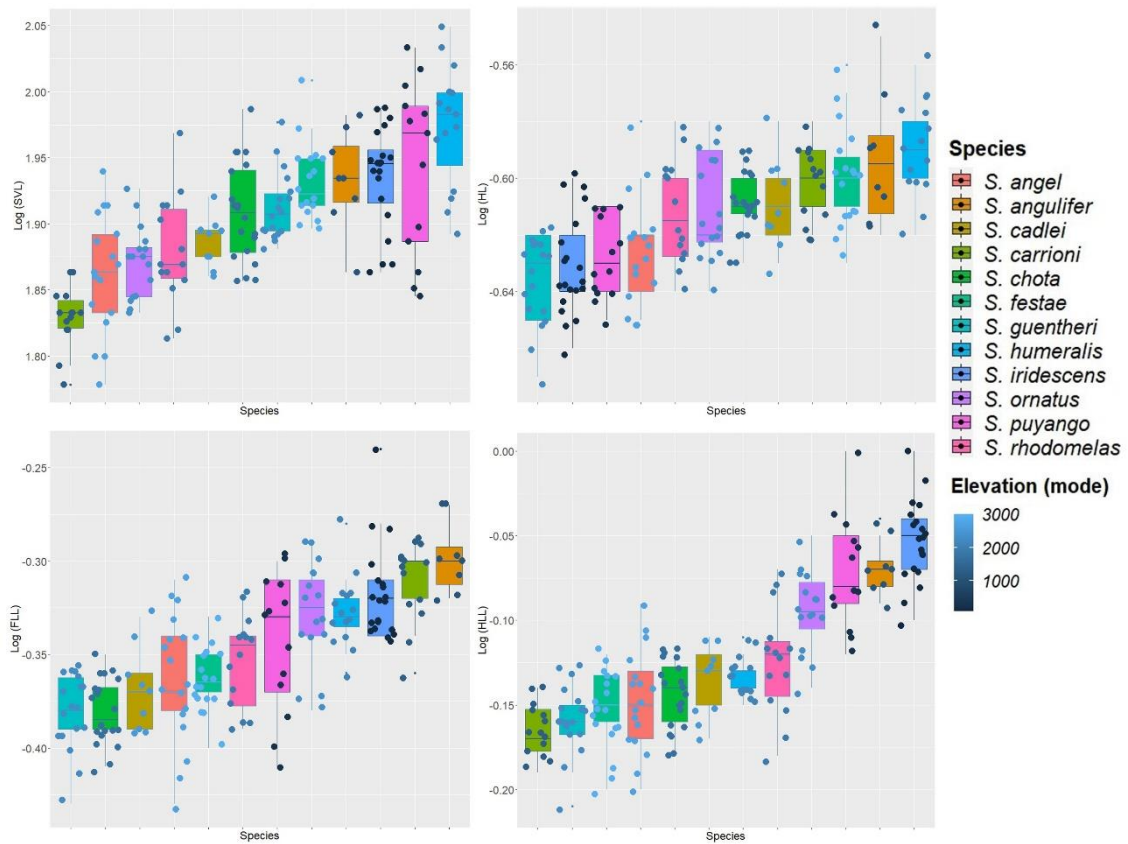


Figure 1. Data distribution of *Stenocercus* measurements. Snout vent length (SVL); Head length (HL); Forelimbs length (FLL); Hindlimbs length (HLL). Species are distinguished by colors and points have blue tones according to their altitudinal distribution.

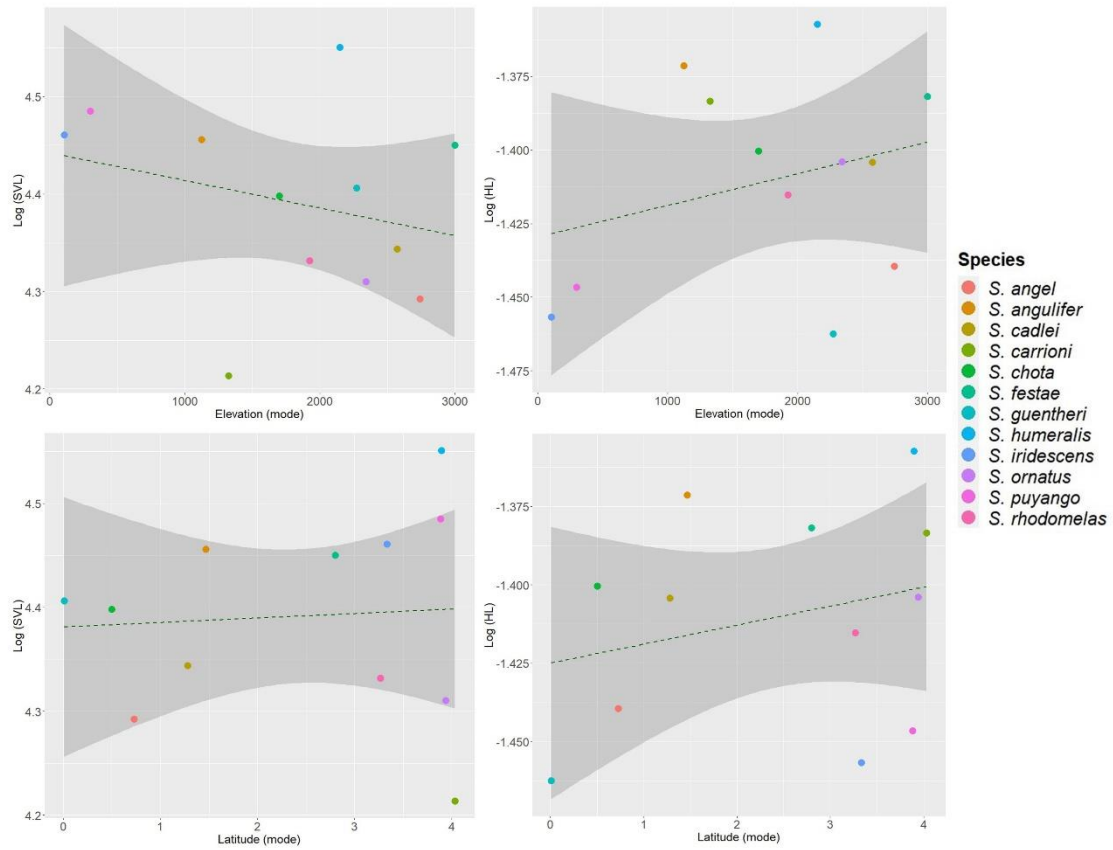


Figure 2. Linear regressions, on the X axis elevation and latitude, and on the Y axis morphological measurements: Snout vent length (SVL), and Head length (HL). Dashed line represents that there is no statistically significant relationship.

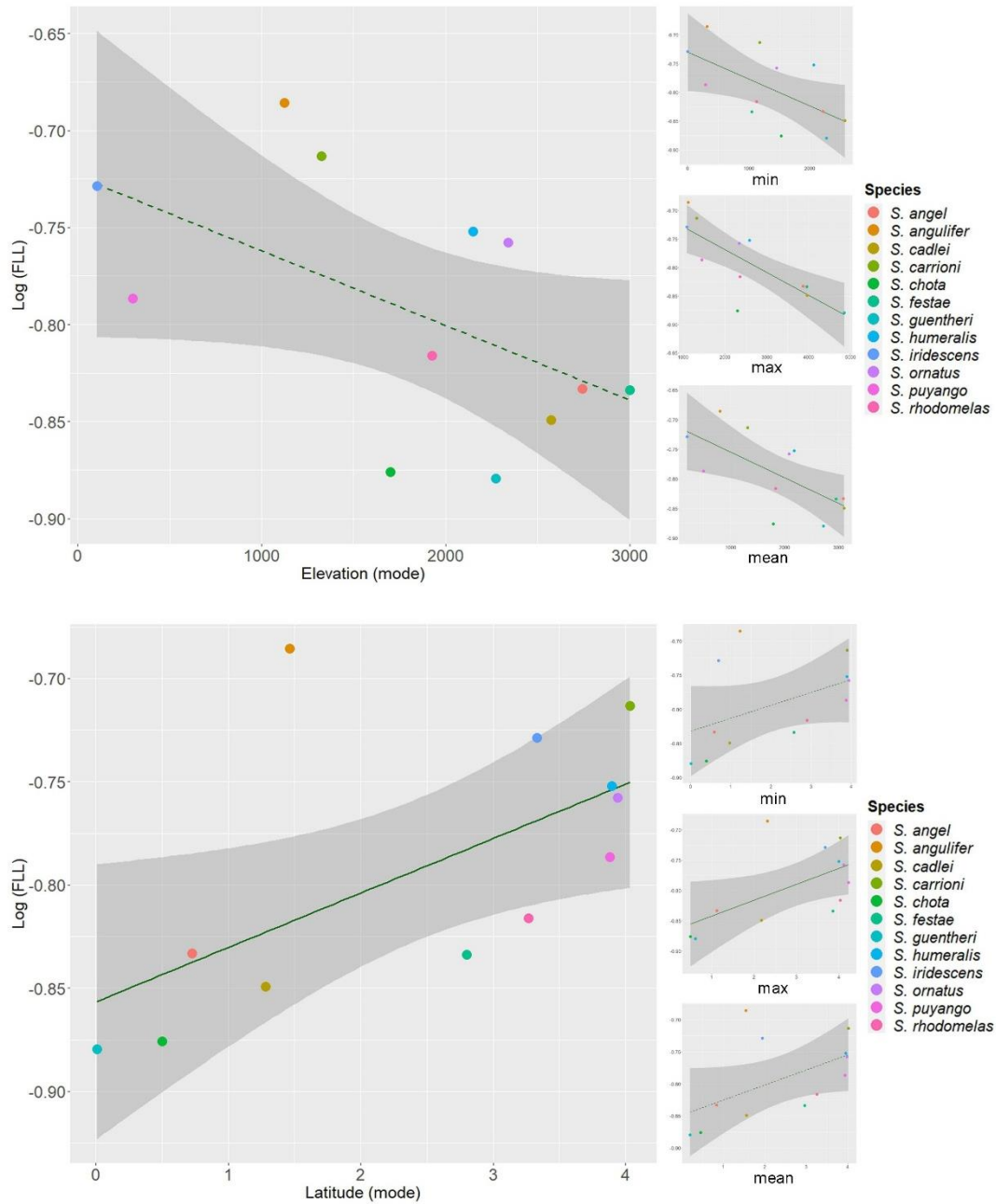


Figure 3. Linear regressions, on the X axis elevation and latitude, and on the Y axis Forelimb length (FLL). Small graphs on the right side were performed with mean, minimum and maximum values of elevation and latitude. Continue line represents that there is a statistically significant relationship and dashed line represents the opposite.

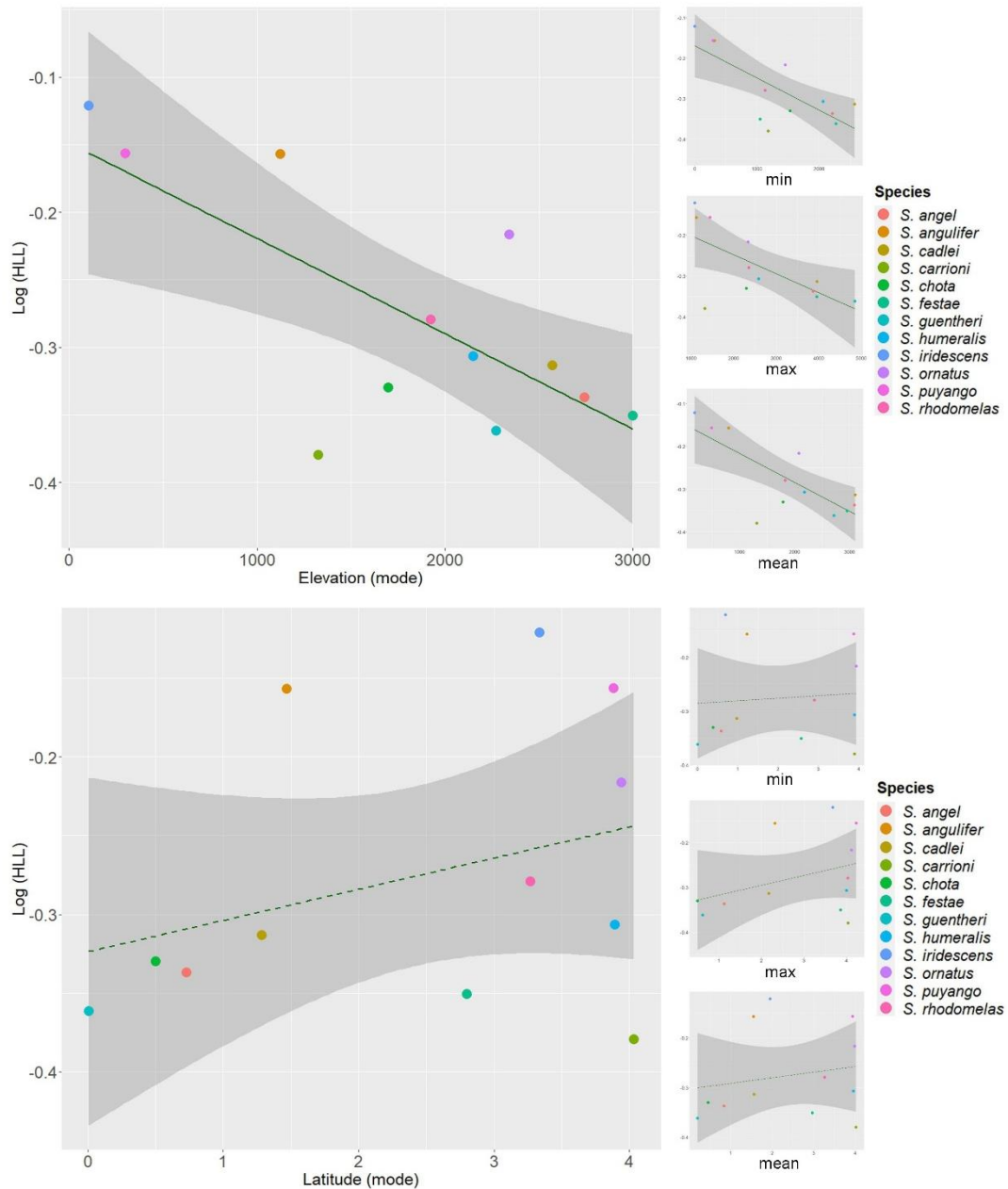


Figure 4. Linear regressions, on the X axis elevation and latitude, and on the Y axis Hindlimb length (HLL). Small graphs on the right side were performed with mean, minimum and maximum values of elevation and latitude. Continue line represents that there is a statistically significant relationship and dashed line represents the opposite.

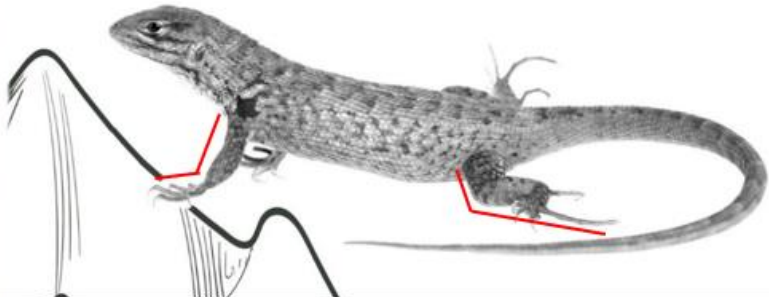
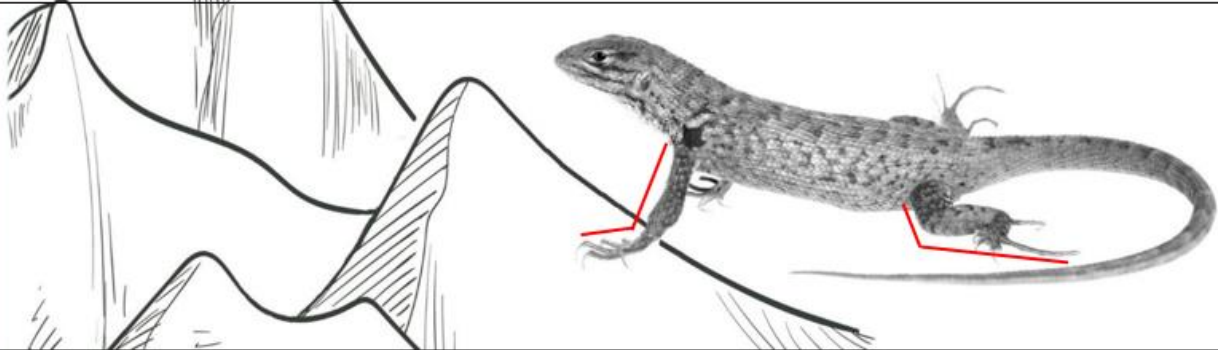
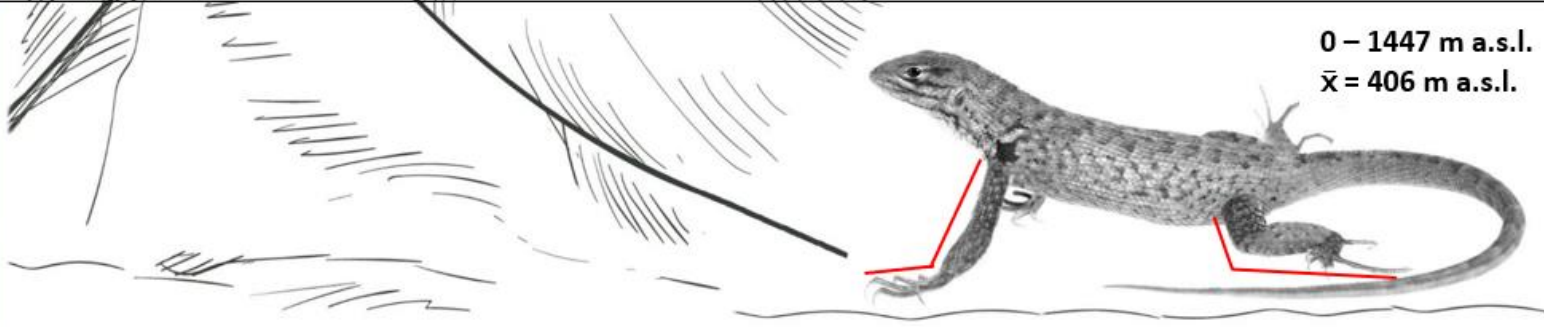
Species		Distribution	Elevation range
Group A	<i>S. angel</i>		1050 – 4851 m a.s.l. \bar{x} = 2942 m a.s.l
	<i>S. cadlei</i>		
	<i>S. festae</i>		
	<i>S. guentheri</i>		
Group B	<i>S. carrioni</i>		1130– 2588 m a.s.l. \bar{x} = 1845 m a.s.l.
	<i>S. chota</i>		
	<i>S. humeralis</i>		
	<i>S. ornatus</i>		
	<i>S. rhodomelas</i>		
Group C	<i>S. iridescens</i>		0 – 1447 m a.s.l. \bar{x} = 406 m a.s.l.
	<i>S. puyango</i>		
	<i>S. angulifer</i>		

Figure 5. *Stenocercus* species grouped by limbs length and elevation range, based on linear models results.

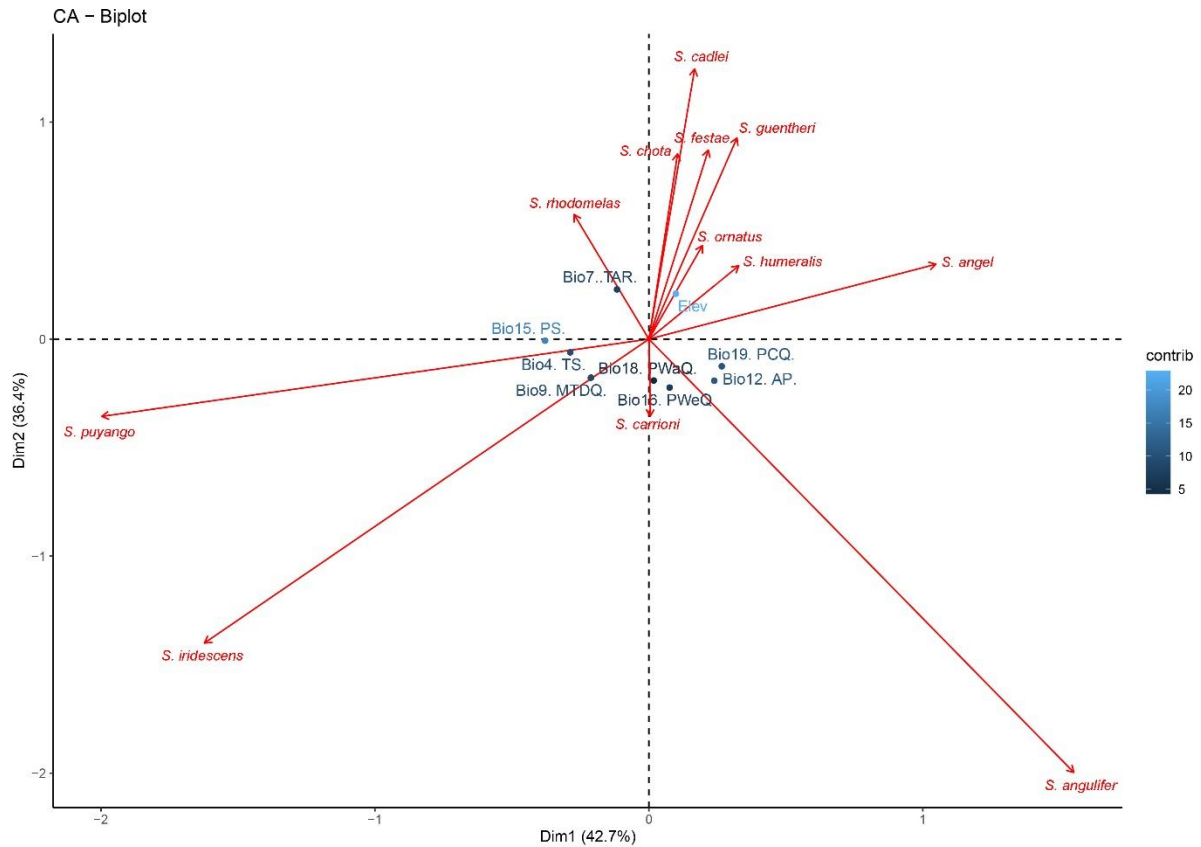


Figure 6. Correspondence analysis biplot using bioclimatic variables and *Stenocercus* species. Symbology: Bio = Bioclimatic variable; TS = Temperature Seasonality; TAR = Temperature Annual Range; MTDQ = Mean Temperature of Driest Quarter, AP = Annual Precipitation; PS = Precipitation Seasonality; PWeQ = Precipitation of Wettest Quarter; PWaQ = Precipitation of Warmest Quarter; PCQ = Precipitation of Coldest Quarter.

Supplementary material

Appendix I.- Shapiro-Wilk test values of standardized morphological measures

	SVL		HL		FLL		HLL	
	W	p-value	W	p-value	W	p-value	W	p-value
<i>Stenocercus angel</i>	0.97852	0.9425	0.947	0.4108	0.95561	0.551	0.96027	0.6366
<i>S. angulifer</i>	0.96825	0.884	0.84697	0.08876	0.95069	0.7181	0.93554	0.5678
<i>S. cadlei</i>	0.93371	0.5174	0.92407	0.427	0.94564	0.6423	0.94192	0.6023
<i>S. carrioni</i>	0.92263	0.2399	0.96182	0.753	0.96384	0.7854	0.96002	0.7235
<i>S. chota</i>	0.94287	0.2715	0.94152	0.2561	0.95171	0.3938	0.96563	0.6613
<i>S. festae</i>	0.88634	0.03342	0.93344	0.2231	0.95585	0.524	0.89908	0.05538
<i>S. guentheri</i>	0.891	0.04014	0.79299	0.001211	0.90329	0.06558	0.95606	0.5277
<i>S. humeralis</i>	0.96648	0.803	0.92527	0.2316	0.94805	0.4942	0.95287	0.5707
<i>S. iridescens</i>	0.92007	0.0994	0.92564	0.1272	0.90853	0.05977	0.96615	0.6724
<i>S. ornatus</i>	0.94369	0.3967	0.94702	0.4439	0.9434	0.3928	0.96271	0.7112
<i>S. puyango</i>	0.91996	0.2505	0.92387	0.2827	0.9076	0.17	0.95159	0.6225
<i>S. rhodomelas</i>	0.94668	0.5105	0.94152	0.4381	0.90746	0.1448	0.90162	0.1191

Appendix II.- Coefficient values of intraspecific allometry linear models

		Estimate	Std. Error	t value	Pr(> t)
<i>Stenocercus angel</i>	HL~SVL	-0.32745	0.06809	-4.809	0.00023
	FLL~SVL	-0.528	0.1506	-3.507	0.00318
	HLL~SVL	-0.4142	0.1323	-3.13	0.00688
<i>S. angulifer</i>	HL~SVL	-0.177	0.2522	-0.702	0.509
	FLL~SVL	-0.2355	0.1869	-1.26	0.254
	HLL~SVL	-0.2914	0.1299	-2.243	0.066
<i>S. cadlei</i>	HL~SVL	-0.05645	0.3005	-0.188	0.856
	FLL~SVL	-0.3305	0.4138	-0.799	0.451
	HLL~SVL	-0.04474	0.42696	-0.105	0.919
<i>S. carrioni</i>	HL~SVL	-0.08281	0.15859	-0.522	0.611
	FLL~SVL	-0.5098	0.214	-2.383	0.0346
	HLL~SVL	-0.4711	0.1372	-3.434	0.00495
<i>S. chota</i>	HL~SVL	-0.08119	0.07029	-1.155	0.2631
	FLL~SVL	-0.142	0.1068	-1.329	0.2
	HLL~SVL	-0.37617	0.09153	-4.11	0.000658
<i>S. festae</i>	HL~SVL	-0.09719	0.1507	-0.645	0.528
	FLL~SVL	-0.1727	0.14192	-1.217	0.241
	HLL~SVL	-0.4722	0.17	-2.777	0.0135
<i>S. guentheri</i>	HL~SVL	-0.06014	0.15181	-0.396	0.6972
	FLL~SVL	-0.3585	0.1665	-2.153	0.0469
	HLL~SVL	-0.3785	0.179	-2.114	0.0506
<i>S. humeralis</i>	HL~SVL	0.23823	0.07205	3.306	0.00568
	FLL~SVL	-0.20889	0.09375	-2.228	0.0441
	HLL~SVL	-0.08734	0.0695	-1.257	0.231
<i>S. iridescens</i>	HL~SVL	-0.34726	0.07131	-4.87	0.000123
	FLL~SVL	-0.415	0.124	-3.347	0.00359
	HLL~SVL	-0.3869	0.1129	-3.427	0.003
<i>S. ornatus</i>	HL~SVL	-0.0562	0.1805	-0.311	0.76
	FLL~SVL	-0.005631	0.269289	-0.021	0.984
	HLL~SVL	-0.1408	0.2331	-0.604	0.555
<i>S. puyango</i>	HL~SVL	-0.1607	0.04302	-3.736	0.00329
	FLL~SVL	-0.4036	0.12	-3.364	0.00632
	HLL~SVL	-0.2928	0.1278	-2.291	0.0427
<i>S. rhodomelas</i>	HL~SVL	-0.25776	0.09569	-2.694	0.0195
	FLL~SVL	-0.2304	0.1633	-1.411	0.184
	HLL~SVL	-0.4826	0.1748	-2.761	0.0173

Appendix IV.- ANOVA's values of interaction and additive models

Interaction model		Df	Sum Sq	Mean Sq	F value	Pr(>F)
FLL~Elev (mode)*β1 (Intra. s.)	Elevation	1	0.01	0.0138693	3.5817	0.09505
	Intraspecific slope	1	0.0013592	0.0013592	0.351	0.5699
	Elev:Intra. slop.	1	0.0000281	0.0000281	0.0073	0.93415
	Residuals	8	0.0309782	0.0038723		
HLL~Elev (mode)*β1 (Intra. s.)	Elevation	1	0.046772	0.046772	13.357	0.00645
	Intraspecific slope	1	0.008106	0.008106	2.3149	0.16663
	Elev:Intra. slop.	1	0.005729	0.005729	1.6361	0.23672
	Residuals	8	0.028013	0.003502		
FLL~Lat (mode)*β1 (Intra. s.)	Latitude	1	0.0177315	0.0177315	5.0163	0.05545
	Intraspecific slope	1	0.0000924	0.0000924	0.0261	0.87557
	Lat:Intra. slop.	1	0.0001327	0.0001327	0.0375	0.85121
	Residuals	8	0.0282784	0.0035348		
HLL~Lat (mode)*β1 (Intra. s.)	Latitude	1	0.010039	0.0100386	1.0597	0.3334
	Intraspecific slope	1	0.002758	0.0027582	0.2911	0.6042
	Lat:Intra. slop.	1	0.000036	0.0000357	0.0038	0.9525
	Residuals	8	0.075787	0.0094734		
Additive model						
FLL~Elev (mode)+β1 (Intra. s.)	Elevation	1	0.0138693	0.0138693	4.0257	0.07576
	Intraspecific slope	1	0.0013592	0.0013592	0.3945	0.54553
	Residuals	9	0.0310064	0.0034452		
HLL~Elev (mode)+β1 (Intra. s.)	Elevation	1	0.046772	0.046772	12.4753	0.006393
	Intraspecific slope	1	0.008106	0.008106	2.1621	0.175527
	Residuals	9	0.033742	0.003749		
FLL~Lat (mode)+β1 (Intra. s.)	Latitude	1	0.0177315	0.0177315	5.6169	0.04191
	Intraspecific slope	1	0.0000924	0.0000924	0.0293	0.86795
	Residuals	9	0.0284111	0.0031568		
HLL~Lat (mode)+β1 (Intra. s.)	Latitude	1	0.010039	0.0100386	1.1916	0.3034

Intraspecific slope	1	0.002758	0.0027582	0.3274	0.5812
Residuals	9	0.075823	0.0084248		

Appendix V.- Environmental variables contribution in correspondence analysis. Variables with the highest contribution are in bold.

	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
Elev	7.69005134	40.7144557	4.1444335	8.475015	0.48577416
Bio19.PCQ.	16.5969853	4.31853634	2.8428036	5.38868	0.01228621
Bio18.PWaQ.	0.06801812	9.27883793	3.6646845	18.514223	0.00729982
Bio16.PWeQ	1.2969349	13.2710509	2.3406473	1.157615	19.3294455
Bio15.PS.	31.7118539	0.01373459	5.1737074	2.992105	32.947712
Bio12.AP.	12.8181247	9.71305763	0.2482182	2.516513	1.50607167
Bio9.MTDQ.	9.60223745	7.96337832	9.6542298	20.301048	35.5924741
Bio7.TAR.	3.03938254	13.8189649	20.6544333	40.07207	7.24304717
Bio4.TS.	17.1764117	0.90798365	51.2768424	0.582732	2.87588939