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Ecological Niche Explains the Sympatric Occurrence of Lined Ground Snakes of the Genus *Lygophis* (Serpentes, Dipsadidae) in the South American Dry Diagonal

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Abstract: The geographic distribution of a species is limited by many factors, including its ecological and evolutionary history. Species distribution modeling has been used to evaluate the effects of climate and other variables on geographic distribution and to measure the degree of niche similarity among co-occurring species. Our goal in this study was to compare the geographic distributions and ecological niches of four closely related species of lined ground snakes, *Lygophis dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens*. These species are distributed along the South American Dry Diagonal. We found that the four species of *Lygophis* overlap somewhat along their distributions with a low degree of niche overlap. *Lygophis dilepis* shows a disjunct distribution with two isolated populations. The break in the distribution of *L. dilepis* in Central Brazil is filled by *L. meridionalis*, which is found mostly in the highlands of the Central Plateau. Because of the disjunct distribution of *L. dilepis*, we performed species distribution modeling on both populations separately. The environmental niches of the two populations of *L. dilepis* were indistinguishable according to the niche equivalence tests, but the distribution of one of these populations did not predict the distribution of the second one, and vice versa. Our study shows that niche partitioning may allow for the coexistence of *Lygophis* species.

Key words: Caatinga; Cerrado; Chaco; Geographic distribution; Potential distribution

The species geographic range is a complex expression of its ecology and evolutionary history, where multiple factors at different scales act to limit distribution (Soberón and Peterson 2005). Detailed data on the spatial distribution of most organisms are scarce, hampering understanding of their conservation status (Giovanelli et al. 2008; Hortal et al. 2015; Tingley et al. 2016a). Sampling gaps in occurrence data, i.e., Wallacean shortfalls, are more evident in megadiverse, developing countries characterized by recent and highly urbanized human occupation (Bini et al. 2006). Biodiversity data are biased and certain groups have received more attention than others, such as large mammals and birds instead of reptiles and amphibians (Hortal et al. 2015). In addition, species occurrence is also biased toward certain regions, habitats, and environmental domains, with biodiversity inventories related to places that offer convenient access, infrastructure, and logistics (Hortal et al. 2015; Guedes et al. 2020). Regarding reptiles, lack of data is more accentuated in tropical regions, especially for fossorial or semifossorial species (Guedes et al. 2018). Accordingly, conservation priorities should focus on regions of high biodiversity value and with data scarceness to reduce extinction risk of species caused mainly by habitat loss (Bini et al. 2006; Hortal et al. 2015).

Species distribution modeling (SDM) has been widely used to forecast the effects of climate change, to evaluate habitat suitability, to support prioritization of conservation areas, and to predict the potential for invasion of exotic species that could constrain biodiversity (Guisan et al. 2017). SDM is a tool for mapping and predicting Wallacean shortfalls for a given species or a set of species, and in addition, it may be used to verify the similarity between niches of different species (Aguirre-Gutiérrez et al. 2015). The SDM allows extrapolation of known points of occurrence of a species to unexplored areas (Guisan and Thuiller 2005). Correlative SDM links occurrence data with environmental variables to build a representation of a species' ecological requirements (Guisan and Thuiller 2005; Elith and Leathwick 2009). In this context, the Grinnellian niche concept is used, that is, the set of environmental conditions required for a species existence at broader geographic scales (Grinnell 1917; Soberón 2007). Ecological niches are projected in environmental spaces, comprising a set of abiotic variables that shape the species' potential occurrence (Elith and Leathwick 2009). Furthermore, niches are converted into geographic distributions by the combination of distribution and abiotic conditions (Soberón and Peterson 2005). Despite the improvements to model species distributions, the development of techniques to quantify overlap of different environmental niches has received relatively little attention (Broennimann et al. 2012).

Sympatry among phylogenetically closely related species may lead to certain ecological pressures, which make them excellent models for hypothesis testing regarding niche overlap and segregation (Pianka 1981; Nogueira et al. 2019a). Resources shared by species indicate niche overlap, which might lead to interspecific competition (Pianka 1981). If they have equal requirements, in the long term, strong pressures can result in character displacement or competitive exclusion (Brown and Wilson 1956; Hardin 1960). This competition can lead one species to overcome the other or

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induce the selection of different ecological traits among them (Brown and Wilson 1956; Hardin 1960). As a consequence, species must differ at least minimally in resource use to coexist (Schoener 1974).

Species groups that are highly diverse with a varied set of ecological adaptations along an environmental gradient are useful for understanding ecological niche differences (Aguirre-Gutiérrez et al. 2015). The Neotropical region harbors more than 880 snake species from 12 families (Guedes et al. 2018). The species richness of snakes is unevenly distributed among ecoregions, with the Cerrado and Caatinga showing outstanding diversity (Roll et al. 2017; Guedes et al. 2018). The knowledge about the biology and geographic distribution of most Neotropical squamates is still incipient, representing a problem for the conservation of the group (Guedes et al. 2018; Tingley et al. 2016b). The *Lygophis lineatus* complex (Dipsadidae, Xenodontinae) comprises five species: *L. dilepis* Cope 1862, *L. flavifrenatus* Cope 1862, *L. lineatus* (Linnaeus 1758), *L. meridionalis* (Schenkel 1901), and *L. paucidens* Hoge 1953. These snakes are distributed in South America, co-occurring in several localities, mainly in the South American Dry Diagonal (sensu Vanzolini 1976), which extends diagonally across a large latitudinal range of South America and includes the Caatinga (northeastern Brazil), the Cerrado savanna (central Brazil), and the Chaco (southwestern South America) domains. Four species (*L. dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens*) have well-known distributions, co-occurring along the South American Dry Diagonal (Guedes et al. 2014, 2018; de Castro and de Oliveira 2017). In contrast, *L. lineatus* is known on the basis of a few records (ca. 35 unique localities) and seems to inhabit forested environments in the northern parts of South America (Dixon 1989; Nogueira et al. 2019b).

The phylogenetic proximity and geographic distribution pattern of the *Lygophis lineatus* complex make the group interesting to investigate niche characteristics and evolution throughout the South American Dry Diagonal. So, herein, we aimed to (1) provide updated distribution maps of *L. dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens*; (2) use SDM to predict geographic ranges; and (3) test for niche overlap among these species. We expected that *L. dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens*, which have partially overlapping distributions, might have different ecological niches, allowing their coexistence and avoiding competition.

Material and Methods

Data Source

We constructed a database of distributional data of the species *Lygophis dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens* by compiling information from specimens from the following scientific collections: Coleção Herpetológica "Alphonse Richard Hoge" do Instituto Butantan, São Paulo; Museu de Zoologia da Universidade de São Paulo, São Paulo; Museu de Zoologia da Universidade Federal da Bahia, Salvador; Coleção Herpetológica da Universidade Federal da Paraíba, João Pessoa; Museu de Zoologia da Universidade Estadual de Feira de Santana, Feira de Santana; Museu Paraense Emílio Goeldi, Belém; Coleção Herpetológica da Universidade Federal do Rio Grande do Norte, Natal; Museu Nacional do Rio de Janeiro, Rio de Janeiro; Coleção Herpetológica da Universidade Federal do Ceará, Fortaleza; Coleção Herpetológica da Universidade de Brasília, Brasília; Museu de Zoologia da Universidade de Campinas, Campinas; Museu de Zoologia "João Moojen" da Universidade Federal de Viçosa, Viçosa; Coleção Herpetológica da Universidade Federal de Mato Grosso do Sul, Campo Grande; Coleção de Répteis, Universidade Federal do Rio Grande do Sul, Porto Alegre; Coleção de Répteis, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; Instituto Nacional de Limnología, Santa Fé; Centro Nacional de Investigaciones Biológicas Malbrán, Buenos Aires; Universidad Nacional del Nordeste Corrientes, Corrientes; Fundación Miguel Lillo, Tucumán; Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; Museo de Historia Natural Noel Kempff Mercado, Santa Cruz; and Museu de História Natural Capão da Imbuia, Curitiba. We complemented the database by including data from the literature (e.g., Dixon 1989; Giraudo 2001; Carreira et al. 2005; Rodrigues 2005; Cacciali 2011; Nogueira et al. 2019b; Serrano et al. 2020). For *L. dilepis* and *L. meridionalis* we also included data collected by us during fieldwork in the states of Rio Grande do Norte, Mato Grosso, and Mato Grosso do Sul, Brazil (Table S1). We identified all specimens to species level on the basis of current taxonomic literature (e.g., Dixon 1989).

In the cases where precise global positioning system (GPS) coordinates were not available, we georeferenced the localities associated with each specimen by consulting gazetteers and the literature, by inspection of georeferenced layers (political division of municipalities, states, and countries limits, drainage systems, protected area limits) in QGIS v2.18.19 (QGIS Core Team 2018). We also obtained precise GPS coordinates for those individuals we collected (SIRGAS 2000 projection).

We classified the species occurrence points in dominion (Löwenberg-Neto 2014; sensu Morrone 2014), country, state/province/department by using the package speciesgeocodeR (Zizka and Antonelli 2015) in R v3.5.1 (R Core Team 2019).

Species Distribution Modeling

Four groups of environmental predictors were used: climate, landscape, topographic, and edaphic variables. We downloaded 19 bioclimatic variables from the WorldClim database (see http://www.worldclim.org/ for variable descriptions) at a resolution of 9 km (Fick and Hijmans 2017), averaged over the 1970–2000 period. The landscape variables consisted of six layers of heterogeneity metrics based on the textural features of the enhanced vegetation index (EVI) imagery extracted from Earth Env (available at https://www.earthenv.org) at a resolution of 5 km (Tuanmu and Jetz 2015). Topographic characteristics across the landscape were attained using the slope/aspect functions under the raster package (Hijmans and Van Etten 2016) that compares the elevation of adjacent cells to compute the average slope and aspect of each grid cell. Also, we added edaphic features (sand fraction) meaningful to *Lygophis* species (e.g., Serrano et al. 2020) obtained from SoilGrids at a resolution of 0.25 km (Hengl et al. 2017; available at https://soilgrids.org/; Supplemental Table S2, available online).

To avoid overprediction and low specificity, we cropped the environmental layers to span from latitude –90 to –30 and longitude –50 to 15 (values in decimal degrees). To reduce autocorrelation among occurrence data and potential for overfitting we eliminated one of each pair of records falling within single grid cells (~3 km) using the package spThin (Aiello-Lammens et al. 2015). To remove problems related to the multicollinearity of the environmental explanatory variables, we calculated the variance inflation factor (VIF) values for variables for each species. All variables that were highly correlated (VIF $>$ 5) were removed through a stepwise procedure using the usdm package (Naimi 2013). Thus, we retained from 11 to 12 variables (Supplemental Table S2).

We performed species distribution modeling using nine different algorithms implemented in the biomod2 package (Thuiller et al. 2009) in R v3.5.1 (R Core Team 2019) including the following: three regression methods (general additive model, Hastie and Tibshirani 1990; general linear model, McCullagh and Nelder 1989; multivariate adaptive regression splines, Friedman 1991); three machine learning methods (generalized boosting model, Ridgeway 1999; maximum entropy, Phillips et al. 2006; and random forest, Breiman 2001); two classification methods (classification tree analysis, Breiman 1984; flexible discriminant analysis, Hastie et al. 1994); and one envelope model (surface range envelop [SRE], Busby 1991). To meet the criteria of having absence (or pseudoabsence [PA]) data for most of these models (except SRE), we generated two equal-sized (to the true presence records) sets of random PA points across the model background (500 PA points in each set). The models were calibrated using 70% of randomly selected data. The other 30% of the data were used for intrinsic model evaluation.

Individual model performance was evaluated using two metrics—true skill statistics (TSS) and the area under the curve of receiver operating characteristics (ROC) implemented in the biomod2 package. TSS is calculated as sensitivity + specificity − 1 and ranges from −1 to +1, where +1 indicates perfect agreement, a value of 0 implies agreement expected by chance, and a value $<$0 indicates agreement lower than expected by chance. Models with high predictive accuracy (TSS $>$ 0.8) were used for the projection of *Lygophis* distribution. We constructed ensemble maps on the basis of the median of two runs of all the selected models in which individual accuracy had TSS value $\geq$0.8 (Table S2). Continuous predictions of ensemble models were transformed into a predicted bivariate map of potential presence versus absence of the species using a threshold approach. Variable importance in the ensemble prediction was evaluated with a permutation procedure (see Thuiller et al. 2009 for details).

Niche Comparisons

We used all bioclimatic predictors at first because tests of niche equivalence/similarity are best performed with the PCA-env method (Broennimann et al. 2012). The PCA-env is calibrated with the full background and reduces environmental data dimensionality to the first two main axes in a principal component analysis (PCA). This full background is then compared with the areas effectively occupied by species on each of its ranges. Kernel density functions were used to produce smoothed densities of both occurrences and environmental availability (Broennimann et al. 2012). The assessment of niche overlap allows quantification the niche shared by *Lygophis* species. In this study, niche overlap between pairs of *Lygophis* species was computed using the Schoener's *D* statistic directly from ecological niche space (Schoener 1968; Warren et al. 2008). The value of *D* ranges between 0, when two species have no overlap in the environmental space, and 1, when two species share the same environmental space.

We used the niche equivalence test to assess whether the ecological niches of pairs of *Lygophis* are significantly different from each other and if the two niche spaces are interchangeable (Warren et al. 2010). We performed a niche equivalence test by comparing the niche overlap values (*D*) of pairs of *Lygophis* species with a null distribution of 100 overlap values because this typically suffices to reject the null hypothesis with high confidence (Hanley and McNeil 1982). The test for niche equivalence is conservative and assesses if two species are identical in their niche space by using their exact locations, without considering the surrounding space. We determined the nonequivalence of ecological niches if the niche overlap value of the species being compared was significantly lower than the overlap values from the null distribution ($P \leq 0.05$).

We also performed a niche similarity test, which assesses if the ecological niches of any pair of species differ from those expected by chance, accounting for differences in the surrounding environmental conditions in the geographic areas where both species are distributed (Warren et al. 2010). Niche similarity tests were first used in Peterson (1999) and test whether niche models calibrated for one species (or population, in our case) predict other species' occurrences better than expected by chance. A significant difference from the niche similarity test would not only indicate differences in the environmental niche space the two species occupy, but also that these differences are not due to the environmental conditions that are geographically available. These analyses were performed in R v3.5.1 (R Core Team 2019) by using the package ecospat (Di Cola et al. 2017).

Lygophis dilepis: A Special Case

During the compilation of distribution points, we recognized that *L. dilepis* has a disjunct distribution, with two isolated populations, one in the northeast and one in the southwest of the South American Dry Diagonal. To verify if these populations have the same pattern of distribution and environmental niche, we analyzed both populations separately (southwest population, *L. dilepis*SW, and northeast population, *L. dilepis*NE) following the same procedures adopted for the other species.

RESULTS

Geographic Distribution

We obtained 435 distribution records for the genus *Lygophis* from the South American Dry Diagonal: 94 records for *L. dilepis* (29 records for *L. dilepis*SW and 65 records for *L. dilepis*NE), 222 for *L. flavifrenatus*, 69 for *L. meridionalis*, and 50 for *L. paucidens* (Table S1).

Lygophis dilepis has a distribution coincident with the South American Dry Diagonal, with records along boreal Brazilian, Chacoan, Parana, and south Brazilian dominions, at altitudes ranging from 6 to 894 m above sea level (a.s.l; Fig. S1). The distribution of *L. dilepis* comprises four countries: Argentina (provinces of Santa Fé, Chaco, Corrientes, and Formosa), Bolivia (department of Santa Cruz), Brazil (states of Alagoas, Bahia, Ceará, Mato Grosso do Sul, Minas Gerais, Paraíba, Pernambuco, Piauí, and Rio Grande do Norte), and Paraguay (departments of Alto Paraguay, Boquerón, Concepción, Cordillera, Misiones, Ñeembucú, Paraguari, and Presidente Hayes; Fig. 1).

Lygophis flavifrenatus is distributed in Chacoan, Parana, and south Brazilian dominions at altitudes ranging from sea level to 1792 m. The updated distribution of *L. flavifrenatus* comprises the following countries: Argentina (provinces of Chaco, Corrientes, Entre Ríos, Formosa, and Misiones), Bolivia (department of Santa Cruz), Brazil (states of Mato Grosso do Sul, Paraná, Rio Grande do Sul, Santa Catarina, and São Paulo), Paraguay (departments of Canindeyú, Itapúa, Misiones, and San Pedro), and Uruguay (departments of Artigas, Paysandú, and Salto; Fig. 1).

Lygophis meridionalis presents the widest distribution among the species considered here, occurring along the boreal Brazilian, Chacoan, Parana, south Brazilian, and southeastern Amazonian dominions at altitudes ranging from 19 to 1313 m a.s.l. (Fig. S1). The updated distribution of *L. meridionalis* comprises the countries of Argentina (provinces of Corrientes and Formosa), Bolivia (departments of Chuquisaca, El Beni, and Santa Cruz), Brazil (states of Bahia, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, São Paulo, and Tocantins), and Paraguay (departments of Amambay, Itapúa, Misiones, Ñeembucú, Presidente Hayes, and San Pedro; Fig. 1).

Lygophis paucidens is distributed in boreal Brazilian, Chacoan, Parana, and south Brazilian dominions at altitudes ranging from sea level to 1161 m. The updated distribution of *L. paucidens* comprises Paraguay (department of San Pedro) and Brazil (states of Mato Grosso, Tocantins, Goiás, Maranhão, Piauí, Ceará, Bahia, Distrito Federal, and Minas Gerais; Fig. 1).

Predicted Geographic Distribution of the Four Species

The resulting ensemble models based on nine SDM algorithms gave averages of TSS = 0.9 and ROC = 0.98 to *L. dilepis*; averages of TSS = 0.95 and ROC = 0.99 to *L. flavifrenatus*; averages of TSS = 0.98 and ROC = 0.99 to *L. meridionalis*; and averages of TSS = 0.93 and ROC = 0.99 to *L. paucidens*.

The predicted distribution of *L. dilepis* was consistent with the occurrence records, confirming the trend of disjunction in the species' geographic distribution (Fig. 1). Annual precipitation was the most important variable (38% of variation explained) for *L. dilepis*, followed by precipitation seasonality (26% of variation explained). Other climate and topographic predictors (precipitation of coldest quarter and elevation) contributed to the *L. dilepis* ecological niche models, though to a lesser extent.

For *L. flavifrenatus*, the predicted geographic distribution indicates similar results with the updated distribution, and also predicted possible occurrence in the western portions of the states of Santa Catarina and Paraná, in southern Brazil, as well as in the region encompassing the coast of the state of São Paulo to the south of Rio de Janeiro (Brazil) and southeast of Minas Gerais. The occurrence of *L. flavifrenatus* in Bolivia and Mato Grosso do Sul (Brazil), reported by Pier Cacciali and with vouchers in the Museo Noel Kempff Mercado (to Bolivia; Amaral 1925) and MCP (to Brazil) collections, was not predicted by the SDM (Fig. 1). The variable isothermality alone was at least two times more important than any other predictor, explaining roughly 51% of the variation in *L. flavifrenatus* distribution. Other climate predictors (minimum temperature of coldest month and precipitation of warmest quarter) helped to explain the *L. dilepis* ecological niche models, though to a lesser extent.

The predicted geographic distribution of *L. meridionalis* indicates a broad range, as shown in the updated distribution (Fig. 1). The SDM also predicted the occurrence of *L. meridionalis* in all states of the south and southeast Brazilian regions, where the species has not been recorded yet. We also registered by literature the occurrence of the species in the septentrional portion of North Brazil and the State of Amazonas, although the SDM niche suitability for this area was low. In addition, the occurrence of *L. meridionalis* was predicted in the northwest portion of Argentina, where it was not recorded. The isothermality was the most important variable (46% of variation explained) to *L. meridionalis*, followed by precipitation of the warmest quarter (30% of variation explained). Other climate predictors (annual precipitation and precipitation of driest month) contributed to the *L. meridionalis* ecological niche models, though to a lesser extent.

For *L. paucidens*, the predicted geographic distribution indicates similar results with the updated distribution, and also predicted possible occurrence in the northeast portion of Mato Grosso and Roraima states in Brazil and northern Bolivia. The occurrence of *L. paucidens* in Paraguay, reported by Cacciali et al. (2013), was not predicted by the SDM (Fig. 1). Isothermality was the most important variable (42% of variation explained) for *L. paucidens*, followed by the coefficient of variation (CV) with 39% of variation explained, which is the normalized dispersion of EVI.

Niche Comparisons

Niche overlap results suggest a considerable amount of overlap in the environmental space inhabited by the *Lygophis* species (Table 1). *Lygophis paucidens* and *L. dilepis* had the highest niche overlap (0.64). However, some species, such as *L. paucidens* and *L. flavifrenatus*, occupy considerably different environmental niches.

For the majority of possible pairwise comparisons between *Lygophis* species, the null hypothesis of the niche equivalency test was rejected (niche equivalency; Table 1). Only the pairwise comparisons between the niche of *L. paucidens* with *L. flavifrenatus* were indistinguishable from each other. In the same way, in our analysis of niche similarity, the null hypothesis was rejected for the majority of pairs of *Lygophis* species (niche similarity; Table 1). The niche similarities for some pairs of *Lygophis* species, especially involving the background of *L. paucidens* and

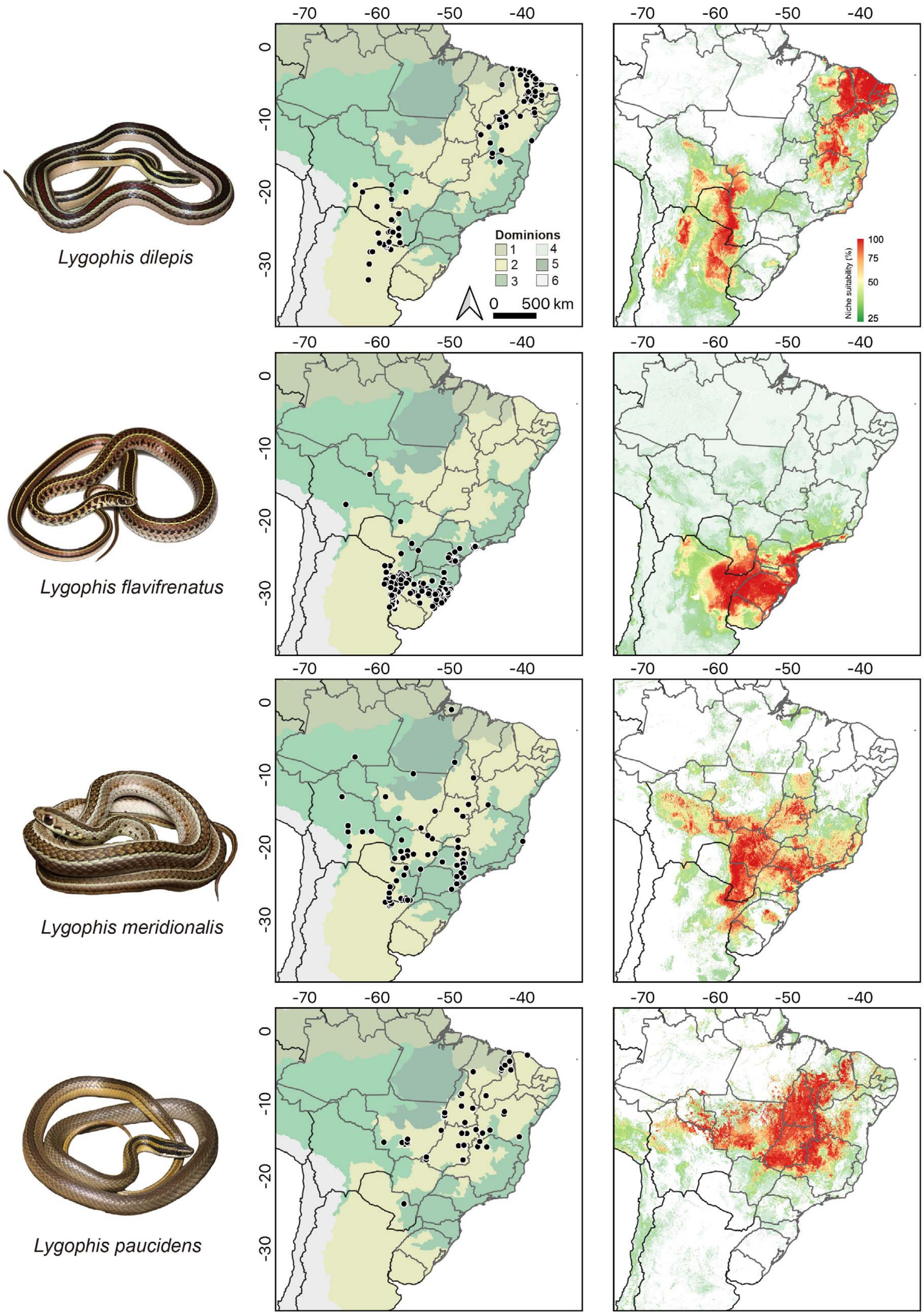

FIG. 1.—Raw distribution (left) and predicted distribution (right) maps of lined ground snakes, genus *Lygophis*, from the Dry Diagonal. Dominions follow Morrone (2014): 1. boreal Brazilian; 2. Chacoan; 3. Parana; 4. south Brazilian; 5. southeastern Amazonian; 6. transition zone. A color version of this figure is available online.

Table 1.—Ecological niche comparisons for *Lygophis* species. Niche overlap values are presented for the comparisons of niche similarity and equivalency of species a with species b. All of the comparisons between *Lygophis* species highlight the nonequivalency of majority ecological niches.

Lygophis species			Similarity		
a	b	Niche overlap (*D*)	a»b	b»a	Equivalence
L. dilepis	*L. meridionalis*	0.616	Similar[a]	Similar[a]	Different[a]
L. dilepis	*L. flavifrenatus*	0.257	ns[b]	Similar[a]	Different[a]
L. flavifrenatus	*L. meridionalis*	0.539	Similar[a]	Similar[a]	Different[a]
L. paucidens	*L. meridionalis*	0.531	ns	Similar[a]	Different[a]
L. paucidens	*L. flavifrenatus*	0.067	ns	Similar[a]	ns
L. paucidens	*L. dilepis*	0.640	Similar[a]	Similar[a]	Different[a]
*L. dilepis*NE	*L. dilepis*SW	0.126	ns	ns	ns

[a] Ecological niches are significantly ($P < 0.05$) more similar or different than expected by chance.

[b] ns = not significantly different.

the comparison between *L. dilepis* and *L. flavifrenatus*, were more similar than expected by chance.

Lygophis dilepis Disjunct Distribution

The break in the distribution of *L. dilepis* is occupied by *L. meridionalis*, which may be related to the high elevation of the Brazilian Shield, a Central Plateau in South America (Fig. S1), because *L. dilepis* does not occur above 900 m a.s.l., whereas *L. meridionalis* can occur up to 1313 m a.s.l. When we modeled separately the two isolated populations of *L. dilepis*, one in the southwest and another in the northeast, the predicted geographic distribution did not cover the entire known occurrence of *L. dilepis* (Fig. 2). The resulting ensemble models based on nine algorithms gave averages of TSS = 0.98 and ROC = 0.99 to *L. dilepis*SW and TSS = 0.95 and ROC = 0.99 to *L. dilepis*NE. The precipitation of the wettest month was the most important variable (48% of variation explained) to *L. dilepis*SW, whereas the annual precipitation was the most important variable (50% of variation explained) to *L. dilepis*NE. Niche overlap between these two populations was low and the null hypotheses of the niche equivalency and similarity tests were rejected (Table 1).

Discussion

The species *Lygophis dilepis*, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens* have some overlap along their distributions and have somewhat similar niches. For *L. dilepis*, the predicted geographic distributions of the southwest and northeast populations, when modeled separately, did not match with the entire occurrence of *L. dilepis*, as would be expected if the two populations represented a single species.

Species distribution models use increasingly sophisticated modeling techniques but often lack detailed examination of the quality of the biological occurrence data on which they are based (Lobo 2008). Here, we performed a vast literature review plus added fieldwork data to improve the known distribution of the four *Lygophis* species studied. We built updated distribution maps for each species through a detailed database (Table S2). Furthermore, recent studies show the importance of fundamental research, such as

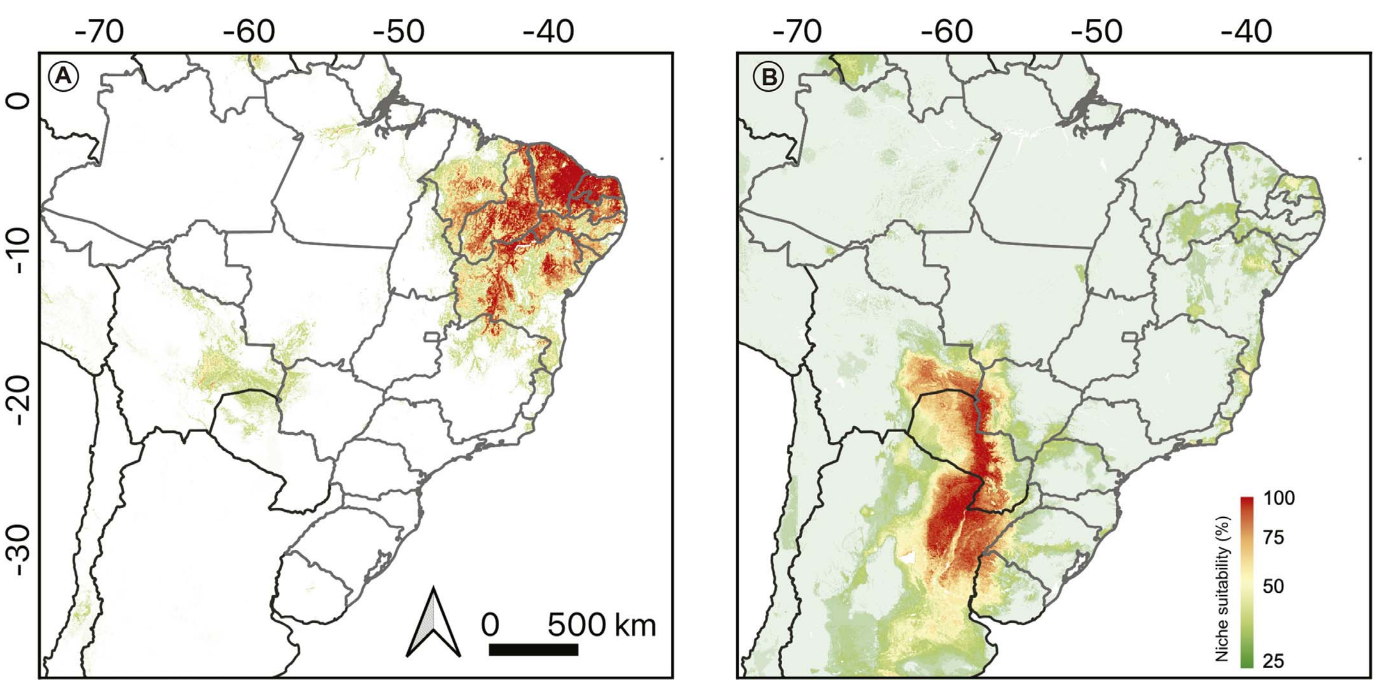

Fig. 2.—Potential geographic distribution of *Lygophis dilepis* based on climatic niche suitability: northeast population (A) and southwest population (B). A color version of this figure is available online.

mapping biodiversity, which is the base for applied research and species conservation (Courchamp et al. 2015). The increased availability of online biodiversity databases has greatly expanded the use of spatial data in science and conservation. The broad availability of spatially referenced species occurrence records along with environmental data has especially enabled us to generate species distribution models from the data set that are readily available on the Internet (Guisan et al. 2017).

Abiotic factors, together with dispersal and biotic interactions, explain the distribution of species and their abundances (Boulangeat et al. 2012). The SDM predicted the occurrence of *Lygophis* species (e.g., *L. meridionalis* in the south and southeast Brazilian regions), on the basis of abiotic factors, where the species has not been recorded yet. The absence of species records in projected occurrence sites by SDM can be related to the impossibility of species to disperse there (e.g., geographic barriers, as in the dispersion of *L. meridionalis* to the central portion of Rio Grande do Sul State, which is separated from the actual species distribution by the Serra Geral mountain chain) or also by the pressure of biotic interaction (e.g., competition; Pulliam 2000).

Climatic variables related to the distribution of *L. dilepis* comprised mostly variables associated with precipitation. For snakes, precipitation can affect the abundance of prey, mainly anurans that are water dependent. In Caatinga Province, anurans, which are the base of the *L. dilepis* diet (Vitt and Vangilder 1983; Michaud and Dixon 1989; Guedes et al. 2014), have become relatively rare and could thus become a limiting resource during drought periods (Vitt 1983). The distributions of *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens* were related to climatic variables of isothermality. Isothermality is the quotient of the differences between the daily and annual temperature ranges. Presence at high values of isothermality may indicate that the species prefers areas where the differences in daily temperature across the day and night are more similar than those across the year. These species are found mainly in the Chaco Dominion that is markedly seasonal, with high levels of temperature variation and thus high isothermality (Prohaska 1976). For example, the Chaco Dominion has extreme daily temperatures ranging from 49°C in summer to –7°C in winter (Prohaska 1976). Also, the distribution of *L. paucidens* was related to a mix of climatic and landscape variables, with the CV the second most important variable. This variable is related to the variation in EVI, associated with habitat heterogeneity (Tuanmu and Jetz 2015).

Lygophis dilepis, *L. flavifrenatus*, *L. meridionalis*, and *L. paucidens* partially overlap in their geographic distributions, and they show a continuum of realized/predicted distribution and similar niches. Given the low variation in environmental conditions where *Lygophis* species occur (Morrone 2014), it is perhaps not surprising that niche overlap among *Lygophis* was relatively high. Niche partitioning has been suggested as one of the main factors segregating distributions of phylogenetically closely related species, mainly through resource competition, although levels of ancestral niche conservatism might also be expected (Wiens and Graham 2005). Conversely, the niche overlap between *L. paucidens* with *L. flavifrenatus* was smaller, which is related to the disparities in species distributions where *L. paucidens* is concentrated in the north of Chaco Dominion and *L. flavifrenatus* in the south.

The ecological niches of *Lygophis* species are partially interchangeable and the differentiation among species may have derived from habitat selection (Luiselli 2006). The species *L. dilepis* and *L. flavifrenatus* show higher niche similarities with *L. meridionalis*. It can be explained by the overlap in distribution by these species with *L. meridionalis*, mainly in Chaco Dominion (Nogueira et al. 2019b). In the same way, niche similarity between *L. dilepis* and *L. paucidens* can be related to the overlap in the distribution of these species in northeast and central-west Brazil (Guedes et al. 2014). Conversely, the differences in niche similarity among *L. paucidens* with *L. flavifrenatus* and *L. meridionalis*, as well as the pairwise comparison between *L. dilepis* and *L. flavifrenatus*, is related to the restricted distribution of *L. paucidens*, which does not cover the entire distribution of *L. meridionalis* in the pairwise comparisons. Differences in niche similarity are also related to the disparity of the distribution of each species, where each species inhabits different regions (Nogueira et al. 2019b).

Our hypothesis of niche equivalence was rejected, which suggests, despite the niche similarities, that their niches are not interchangeable. To avoid total overlap, decrease competition, and allow coexistence, species with the same distribution usually exploit the environment differently (Schoener 1974). Among snakes, species inhabiting the same area may differ in their habitat selection, trophic niche, and period of activity (Strüssmann and Sazima 1993; Borges and Araujo 1998; França et al. 2008; Sawaya et al. 2008). The principle of competitive exclusion demonstrates that species cannot coexist if they have the same requirements (Hardin 1960). Thus, habitat partitioning may avoid interspecific competition, permitting the coexistence of species with similar requirements, resulting in a highly diverse community (Schoener 1974). The *L. lineatus* complex demonstrates that they have similar spatial niches; however, despite habitat partitioning, the trophic niche and activity periods may show some differences. In general, tropical snakes partition the food resource (prey type or prey size), but when this resource is not partitioned competitive exclusion can occur (Luiselli 2006). For instance, *L. dilepis* is the only species with a diet specialized in anurans (Vitt and Vangilder 1983; Michaud and Dixon 1989; Guedes et al. 2014), whereas *L. paucidens* preys mostly on lizards of the family Teiidae and *L. flavifrenatus* and *L. meridionalis* are generalists preying upon anurans, lizards, and birds (Michaud and Dixon 1989; Sawaya et al. 2008). Thus the niche partitioning and coexistence among *Lygophis* species, mainly in Chaco Dominion, is potentially allowed by the difference in the trophic niche, habitat selection, and period of activity.

Lygophis dilepis: A Special Case

Regarding *L. dilepis*, the predicted geographic distribution of the southwestern and northeastern populations did not match with the entire occurrence of *L. dilepis*, as expected by a single species. The disjunct distribution of *L. dilepis* may reflect the presence of two distinct species under the same name. The environmental niches of *L. dilepis*SW and *L. dilepis*NE are indistinguishable according to the niche equivalence test, but the distribution of one of these species does not predict the distribution of the second one, and vice versa. Some authors have suggested, on the basis of parsimony analysis of endemicity of birds and lizards, that the Caatinga, Cerrado, and Chaco provinces form a natural biogeographic region (Colli 2005; Porzecanski and Cracraft 2005). Similar to our findings for *L dilepis*, other taxa also show a disjunct distribution, occurring in both Caatinga and Chaco provinces, but not in the Cerrado (Bucher 1982). Similar patterns of distribution in other taxa across the South American Dry Diagonal are known, as for *Lygodactylus* spp. (Lanna et al. 2018), *Phyllopezus* spp. (Gamble et al. 2012), *Vanzosaura* spp. (Recoder et al. 2014), *Ameivula* gr. *ocellifera* (Oliveira, pers. comm.), and *Dermatonotus muelleri* (Oliveira et al. 2018). Accordingly, the similar disjunct distribution of *L. dilepis* may reflect the presence of two distinct species under the same name but with a common ancestor. However, as found for species with similar distribution patterns (e.g., Gamble et al. 2012; Recoder et al. 2014), it is necessary to use an integrative taxonomy approach that involves molecular, phylogenetic, morphologic, and geographic variation data for proper species delimitation (ongoing study led by TBG).

Taxonomy and conservation go hand in hand because we cannot necessarily expect to conserve organisms that we cannot identify and know where they are distributed (Godfray et al. 2004). Thus, a well-resolved and well-supported taxonomy and a good database of species occurences are the basis for comprehending species distribution patterns around the globe. Using an extensive database, we demonstrated that *Lygophis* species inhabiting the South American Dry Diagonal have similar but not interchangeable niches, which allow their co-occurrence in some areas, mainly in the boundaries of the dominions, as in the Chaco dominion. In addition, we demonstrated that *L. dilepis* has a disjunct population distribution, with evidence for different requirements and habitat use suggesting potential regional speciation.

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Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-20-00056.S1

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Ecological niche explains the sympatric occurrence of lined ground snakes of the genus *Lygophis* (Serpentes, Dipsadidae) in the South American Dry Diagonal

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SUPPORTING INFORMATION

Supplementary Material S1

Fig. 1.S1: *Lygophis dilepis* (green dots) and *L. meridionalis* (blue dots) distribution along elevation gradient throughout the Dry Diagonal

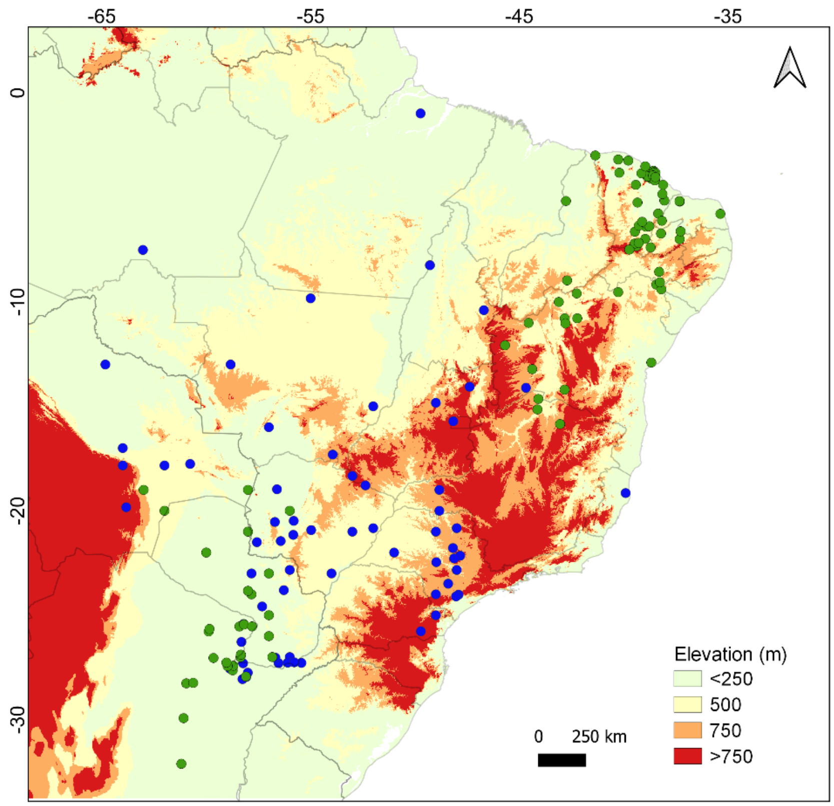

Table 1.S1. Distribution records of *Lygophis dilepis*, *L. flavifrenatus*, *L. meridionalis* and *L. paucidens* compiled in this study. See material and methods section of the paper to access scientific collections acronyms, and reference section of this supplementary material to access the details of the literature source numbered from 1 to 44 in this table.

Species	Lat	Long	Elevation	Country, State/Department	Ecoregion (dominion)	Source
L. dilepis	-28.24	-60.62	63	Argentina, Santa Fe	Chacoan dominion	[1]
L. dilepis	-27.43	-58.97	52	Argentina, Chaco	Chacoan dominion	[1]
L. dilepis	-27.27	-59.03	54	Argentina, Chaco	Chacoan dominion	[1]
L. dilepis	-27.04	-59.65	71	Argentina, Chaco	Chacoan dominion	[1]
L. dilepis	-27.42	-58.7	61	Argentina, Corrientes	Chacoan dominion	[1]
L. dilepis	-27.64	-58.73	65	Argentina, Corrientes	Chacoan dominion	[1]
L. dilepis	-27.93	-58.1	76	Argentina, Corrientes	Chacoan dominion	[1]
L. dilepis	-25.54	-57.8	62	Argentina, Formosa	Chacoan dominion	[1]
L. dilepis	-25.44	-58.19	72	Argentina, Formosa	Chacoan dominion	[1]
L. dilepis	-25.54	-58.41	81	Argentina, Formosa	Chacoan dominion	[1]
L. dilepis	-25.78	-59.88	101	Argentina, Formosa	Chacoan dominion	[1]
L. dilepis	-25.66	-59.84	104	Argentina, Formosa	Chacoan dominion	[1]
L. dilepis	-32.11	-61.19	40	Argentina, Santa Fe	Chacoan dominion	[1]
L. dilepis	-28.26	-60.95	64	Argentina, Santa Fe	Chacoan dominion	[1]
L. dilepis	-29.93	-61.08	66	Argentina, Santa Fe	Chacoan dominion	[1]
L. dilepis	-19	-58	111	Bolivia, Santa Cruz	South Brazilian dominion	[2]
L. dilepis	-20	-62	371	Bolivia, Santa Cruz	Chacoan dominion	[2]
L. dilepis	-19	-63	405	Bolivia, Santa Cruz	Chacoan dominion	[2]
L. dilepis	-9.4	-38.2	184	Brazil, Bahia	Chacoan dominion	MZUFBA [36]
L. dilepis	-12.91	-38.68	36	Brazil, Bahia	Chacoan dominion	IBSP [36]
L. dilepis	-9.18	-38.44	362	Brazil, Bahia	Chacoan dominion	ZUEC [36]
L. dilepis	-9.54	-40.27	388	Brazil, Bahia	Chacoan dominion	MZUEFS, IBSP [36]
L. dilepis	-11.03	-42.79	406	Brazil, Bahia	Chacoan dominion	IBSP [36]
L. dilepis	-9.6	-42.25	409	Brazil, Bahia	Chacoan dominion	IBSP [36]

L. dilepis	-10.79	-42.83	412	Brazil, Bahia	Chacoan dominion	MZUFBA, MZUSP [36]
L. dilepis	-10.79	-42.22	422	Brazil, Bahia	Chacoan dominion	IBSP [36]
L. dilepis	-10.01	-43.11	437	Brazil, Bahia	Chacoan dominion	MZUFBA [36]
L. dilepis	-11.01	-44.56	441	Brazil, Bahia	Chacoan dominion	MZUSP [36]
L. dilepis	-14.2	-42.83	512	Brazil, Bahia	Chacoan dominion	MZUFV [36]
L. dilepis	-13.22	-44.38	740	Brazil, Bahia	Parana dominion	CHUNB [36]
L. dilepis	-12.08	-45.69	757	Brazil, Bahia	Chacoan dominion	MNRJ [36]
L. dilepis	-3.75	-38.63	6	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.79	-38.53	13	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.52	-38.97	27	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.24	-39.78	29	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.73	-38.57	30	Brazil, Ceará	Chacoan dominion	MPEG [36]
L. dilepis	-5.15	-38.05	31	Brazil, Ceará	Chacoan dominion	CHUFC, IBSP [36]
L. dilepis	-3.82	-38.48	36	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-4.84	-38.15	39	Brazil, Ceará	Chacoan dominion	CHUFC, MNRJ [36]
L. dilepis	-3.85	-38.57	42	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4.4	-38.11	42	Brazil, Ceará	Chacoan dominion	MZUSP [36]
L. dilepis	-3.88	-38.63	49	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4.03	-38.48	55	Brazil, Ceará	Chacoan dominion	MZUSP [36]
L. dilepis	-3.95	-38.6	59	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.19	-40.26	68	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.78	-38.81	73	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4.11	-38.68	84	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4.19	-38.51	86	Brazil, Ceará	Chacoan dominion	MZUSP [36]
L. dilepis	-3.85	-39.15	94	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-3.82	-40.21	113	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4.02	-38.87	116	Brazil, Ceará	Chacoan dominion	MZUSP [36]
L. dilepis	-5.78	-38.35	131	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-4	-38.82	142	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-6.38	-38.78	194	Brazil, Ceará	Chacoan dominion	IBSP [36]

L. dilepis	-6.36	-39.28	208	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-6.17	-39.12	213	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-6.4	-38.95	218	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-6.64	-39.47	255	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-4.4	-39.42	265	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-6.99	-38.97	311	Brazil, Ceará	Chacoan dominion	CHUFC [36]
L. dilepis	-5.25	-39.34	348	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-7.18	-39.28	396	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-7.4	-38.71	410	Brazil, Ceará	Chacoan dominion	CHUFC, MNRJ [36]
L. dilepis	-7.33	-39.38	562	Brazil, Ceará	Chacoan dominion	MZUSP [36]
L. dilepis	-7.21	-39.48	894	Brazil, Ceará	Chacoan dominion	IBSP [36]
L. dilepis	-20	-56	126	Brazil, Mato Grosso do Sul	South Brazilian dominion	[2]
L. dilepis	-15.15	-44.13	456	Brazil, Minas Gerais	Parana dominion	CHUFC [36]
L. dilepis	-14.65	-44.09	469	Brazil, Minas Gerais	Parana dominion	MNRJ [36]
L. dilepis	-15.85	-43.05	603	Brazil, Minas Gerais	Chacoan dominion	MZUFV [36]
L. dilepis	-6.73	-38.21	220	Brazil, Paraíba	Chacoan dominion	MNRJ [36]
L. dilepis	-7	-37.32	249	Brazil, Paraíba	Chacoan dominion	IBSP [36]
L. dilepis	-8.56	-38.31	377	Brazil, Pernambuco	Chacoan dominion	ZUEC [36]
L. dilepis	-9.07	-38.27	384	Brazil, Pernambuco	Chacoan dominion	CHUFPB [36]
L. dilepis	-7.5	-39.73	527	Brazil, Pernambuco	Chacoan dominion	MZUSP [36]
L. dilepis	-2.99	-41.36	23	Brazil, Piauí	Chacoan dominion	MNRJ [36]
L. dilepis	-5.17	-42.77	115	Brazil, Piauí	Boreal Brazilian dominion	IBSP [36]
L. dilepis	-8.98	-42.71	385	Brazil, Piauí	Chacoan dominion	IBSP [36]
L. dilepis	-5.18	-37.33	10	Brazil, Rio Grande do Norte	Chacoan dominion	CHUFC [36]
L. dilepis	-5.18	-37.33	10	Brazil, Rio Grande do Norte	Chacoan dominion	IBSP [36]
L. dilepis	-5.18	-37.32	13	Brazil, Rio Grande do Norte	Chacoan dominion	CHUFC [36]
L. dilepis	-5.79	-35.37	14	Brazil, Rio Grande do Norte	Chacoan dominion	IBSP [36]
L. dilepis	-5.2	-37.32	19	Brazil, Rio Grande do Norte	Chacoan dominion	CHUFC [36]
L. dilepis	-6.63	-37.28	203	Brazil, Rio Grande do Norte	Chacoan dominion	CHBEZ, CHUNB [36]
L. dilepis	-6.12	-38.17	260	Brazil, Rio Grande do Norte	Chacoan dominion	MPEG [36]

L. dilepis	-21	-58	84	Paraguay, Alto Paraguay	South Brazilian dominion	[2]
L. dilepis	-22	-60	142	Paraguay, Boquerón	Chacoan dominion	[2]
L. dilepis	-23	-57	120	Paraguay, Concepción	Chacoan dominion	[2]
L. dilepis	-25	-57	63	Paraguay, Cordillera	Chacoan dominion	[2]
L. dilepis	-27	-56.83	164	Paraguay, Misiones	Chacoan dominion	[2]
L. dilepis	-27.01	-58.36	57	Paraguay, Ñeembucú	Chacoan dominion	[1]
L. dilepis	-26.89	-58.34	57	Paraguay, Ñeembucú	Chacoan dominion	[1]
L. dilepis	-26	-57	123	Paraguay, Paraguarí	Parana dominion	[2]
L. dilepis	-24	-57.83	81	Paraguay, Presidente Hayes	Chacoan dominion	[2]
L. dilepis	-23.83	-58	83	Paraguay, Presidente Hayes	Chacoan dominion	[2]
L. flavifrenatus	-27.05	-58.68	58	Argentina, Chaco	Chacoan dominion	[3]
L. flavifrenatus	-27.08	-58.73	59	Argentina, Chaco	Chacoan dominion	MNRJ
L. flavifrenatus	-28.93	-56.42	54	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-29.1	-56.58	55	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-29.47	-56.83	56	Argentina, Corrientes	Chacoan dominion	CENAI
L. flavifrenatus	-28.53	-56.05	56	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.53	-56.05	56	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-29.12	-56.6	56	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-28.63	-56.68	57	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-28.65	-58.79	58	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.7	-56.18	60	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.47	-56.02	60	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.88	-58.47	61	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-29.1	-56.55	64	Argentina, Corrientes	Chacoan dominion	CENAI
L. flavifrenatus	-29.47	-56.82	64	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.55	-57.2	65	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-29.51	-57.56	65	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.51	-58.05	65	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.1	-58.78	65	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.71	-59	65	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.53	-57.17	66	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.58	-59.03	67	Argentina, Corrientes	Chacoan dominion	INALI

L. flavifrenatus	-28.83	-56.33	68	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28	-58.57	68	Argentina, Corrientes	Chacoan dominion	MNRJ
L. flavifrenatus	-28.1	-56.97	69	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-27.83	-57.92	70	Argentina, Corrientes	Chacoan dominion	CENAI
L. flavifrenatus	-28.37	-56.86	70	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.37	-56.84	71	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.74	-57.77	71	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-30.24	-57.97	71	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-27.6	-56.7	72	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.68	-57.39	72	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.65	-57.36	72	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-27.94	-57.53	73	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.6	-56.68	73	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-28.25	-58.62	74	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-28.35	-56.83	74	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.25	-58.62	74	Argentina, Corrientes	Chacoan dominion	MNRJ
L. flavifrenatus	-28.25	-58.62	74	Argentina, Corrientes	Chacoan dominion	MNRJ
L. flavifrenatus	-28.1	-56.69	75	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-27.6	-56.69	77	Argentina, Corrientes	Chacoan dominion	FML
L. flavifrenatus	-30.18	-58.15	77	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.62	-57.17	78	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.97	-56.54	81	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-28.49	-56.04	82	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.85	-56.49	83	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.73	-56.47	86	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-27.86	-56.49	89	Argentina, Corrientes	Chacoan dominion	UNNEC
L. flavifrenatus	-27.6	-56.3	94	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.51	-56.06	100	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-29.21	-58.11	102	Argentina, Corrientes	Chacoan dominion	[3]
L. flavifrenatus	-29.26	-58.14	104	Argentina, Corrientes	Chacoan dominion	INALI
L. flavifrenatus	-28.22	-56.13	110	Argentina, Corrientes	Chacoan dominion	CENAI
L. flavifrenatus	-31.88	-58.25	36	Argentina, Entre Ríos	Chacoan dominion	[3]

L. flavifrenatus	-31.87	-58.28	36	Argentina, Entre Ríos	Chacoan dominion	MACN
L. flavifrenatus	-31.87	-58.28	36	Argentina, Entre Ríos	Chacoan dominion	Pier Cacciali
L. flavifrenatus	-31.87	-58.28	36	Argentina, Entre Ríos	Chacoan dominion	[3]
L. flavifrenatus	-26.18	-58.18	63	Argentina, Formosa	Chacoan dominion	CENAI
L. flavifrenatus	-26.17	-58.93	76	Argentina, Formosa	Chacoan dominion	REB
L. flavifrenatus	-26.17	-58.93	76	Argentina, Formosa	Chacoan dominion	REB
L. flavifrenatus	-26.17	-58.93	76	Argentina, Formosa	Chacoan dominion	UNNEC
L. flavifrenatus	-27.38	-55.9	105	Argentina, Misiones	Parana dominion	CENAI
L. flavifrenatus	-27.38	-55.9	105	Argentina, Misiones	Parana dominion	CENAI
L. flavifrenatus	-27.38	-55.9	105	Argentina, Misiones	Parana dominion	[3]
L. flavifrenatus	-27.37	-55.9	121	Argentina, Misiones	Parana dominion	[3]
L. flavifrenatus	-27.98	-55.52	171	Argentina, Misiones	Chacoan dominion	CENAI
L. flavifrenatus	-13.58	-61	171	Bolivia, Santa Cruz	South Brazilian dominion	Pier Cacciali
L. flavifrenatus	-17.72	-64.3	1722	Bolivia, Santa Cruz	South Brazilian dominion	MNKR
L. flavifrenatus	-20.08	-56.75	115	Brazil, Mato Grosso do Sul	South Brazilian dominion	[4]
L. flavifrenatus	-23.12	-55.22	471	Brazil, Mato Grosso do Sul	Parana dominion	MCP
L. flavifrenatus	-24.68	-50.02	18	Brazil, Paraná	Parana dominion	MHNCI
L. flavifrenatus	-25.4	-49.73	59	Brazil, Paraná	Parana dominion	MHNCI
L. flavifrenatus	-24.95	-50.12	60	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-24.92	-50.1	139	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.62	-49.74	863	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.59	-49.41	875	Brazil, Paraná	Parana dominion	[5]
L. flavifrenatus	-25.53	-49.21	880	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.58	-49.4	909	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.42	-49.27	909	Brazil, Paraná	Parana dominion	MHNCI
L. flavifrenatus	-25.08	-50.17	932	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.43	-49.82	952	Brazil, Paraná	Parana dominion	MHNCI
L. flavifrenatus	-25.47	-49.53	953	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.1	-50.16	975	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-24.79	-50.01	990	Brazil, Paraná	Parana dominion	IBSP
L. flavifrenatus	-25.29	-49.23	993	Brazil, Paraná	Parana dominion	MHNCI
L. flavifrenatus	-32.12	-52.15	1	Brazil, Rio Grande do Sul	Chacoan dominion	MCN

L. flavifrenatus	-29.98	-50.13	1	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-29.32	-49.75	2	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-31.37	-51.97	3	Brazil, Rio Grande do Sul	Chacoan dominion	[6]
L. flavifrenatus	-31	-51.58	4	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.97	-50.13	4	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.9	-50.08	4	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-30.17	-51.22	4	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.35	-49.73	4	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.63	-49.94	5	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.64	-49.95	5	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.58	-49.91	6	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.75	-50.02	6	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-30.33	-50.28	6	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-30.36	-50.28	6	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.34	-49.73	6	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-32.04	-52.1	7	Brazil, Rio Grande do Sul	Chacoan dominion	[6]
L. flavifrenatus	-29.37	-49.76	7	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.76	-51.15	7	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-32.04	-52.1	7	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.28	-50.26	8	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-30.38	-51.03	8	Brazil, Rio Grande do Sul	Chacoan dominion	UFRGS
L. flavifrenatus	-29.75	-50.01	8	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.8	-50.04	8	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-29.48	-49.84	9	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.48	-49.84	9	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.86	-51.18	9	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.18	-50.21	10	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.99	-51.08	10	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.48	-50.47	11	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.77	-51.15	11	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-30.39	-50.32	14	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-30.21	-51.18	14	Brazil, Rio Grande do Sul	Chacoan dominion	MCN

L. flavifrenatus	-31.77	-52.34	15	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-31.29	-51.09	15	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.69	-51.46	15	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-31.77	-52.34	15	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.95	-50.72	17	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.89	-50.27	17	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-30.92	-50.75	18	Brazil, Rio Grande do Sul	Chacoan dominion	[5]
L. flavifrenatus	-30.08	-51.62	21	Brazil, Rio Grande do Sul	Chacoan dominion	UFRGS
L. flavifrenatus	-29.92	-51.18	23	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.92	-51.18	23	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.97	-51.8	27	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.82	-51.92	29	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-29.94	-50.99	29	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.85	-51.81	35	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.81	-53.38	38	Brazil, Rio Grande do Sul	Parana dominion	IBSP
L. flavifrenatus	-30.03	-51.23	38	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-30.12	-51.95	50	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-30.26	-52.8	52	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-30.1	-51.65	52	Brazil, Rio Grande do Sul	Chacoan dominion	UFRGS
L. flavifrenatus	-29.67	-52.79	57	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-30.04	-52.89	59	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-30.12	-51.96	61	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-28.59	-55.96	73	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.77	-57.08	75	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-30.12	-51.17	76	Brazil, Rio Grande do Sul	Chacoan dominion	MCP
L. flavifrenatus	-30.12	-51.17	76	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-28.17	-55.64	81	Brazil, Rio Grande do Sul	Chacoan dominion	UNNEC
L. flavifrenatus	-29.78	-55.12	82	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-29.95	-54.95	84	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-30.03	-52.9	85	Brazil, Rio Grande do Sul	Parana dominion	IBSP
L. flavifrenatus	-29.79	-55.1	92	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-29.72	-53.72	93	Brazil, Rio Grande do Sul	Parana dominion	[7]

L. flavifrenatus	-30.08	-51.02	95	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.88	-54.83	106	Brazil, Rio Grande do Sul	Chacoan dominion	[6]
L. flavifrenatus	-30.33	-54.32	109	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-29.68	-53.81	132	Brazil, Rio Grande do Sul	Parana dominion	IBSP
L. flavifrenatus	-29.68	-53.81	132	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.83	-50.93	134	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.98	-55.42	175	Brazil, Rio Grande do Sul	Chacoan dominion	UFRGS
L. flavifrenatus	-31.33	-54.11	200	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-28.73	-54.9	251	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-29.33	-53.09	337	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-28.56	-53.96	350	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-28.65	-53.6	441	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-29.08	-53.83	449	Brazil, Rio Grande do Sul	Chacoan dominion	IBSP
L. flavifrenatus	-28.64	-53.61	454	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-28.26	-52.41	661	Brazil, Rio Grande do Sul	Chacoan dominion	MCN
L. flavifrenatus	-28.25	-52.33	691	Brazil, Rio Grande do Sul	Chacoan dominion	[8]
L. flavifrenatus	-29.17	-51.18	790	Brazil, Rio Grande do Sul	Parana dominion	IBSP
L. flavifrenatus	-29.45	-50.58	892	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.45	-50.58	892	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-29.38	-50.43	902	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-29.4	-50.32	925	Brazil, Rio Grande do Sul	Parana dominion	MCP
L. flavifrenatus	-28.5	-50.93	947	Brazil, Rio Grande do Sul	Parana dominion	UFRGS
L. flavifrenatus	-28.51	-50.93	962	Brazil, Rio Grande do Sul	Parana dominion	MCN
L. flavifrenatus	-27.11	-50.76	854	Brazil, Santa Catarina	Parana dominion	[9]
L. flavifrenatus	-28.09	-50.75	935	Brazil, Santa Catarina	Parana dominion	[9]
L. flavifrenatus	-24.27	-49.27	73	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.8	-48.6	601	Brazil, São Paulo	Parana dominion	[6]
L. flavifrenatus	-23.58	-46.7	725	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.51	-46.88	726	Brazil, São Paulo	Parana dominion	[5]
L. flavifrenatus	-23.55	-46.25	740	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.49	-46.44	740	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.5	-46.57	741	Brazil, São Paulo	Parana dominion	IBSP

L. flavifrenatus	-23.5	-46.88	744	Brazil, São Paulo	Parana dominion	[6]
L. flavifrenatus	-23.43	-46.47	746	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.57	-46.72	746	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.58	-46.61	748	Brazil, São Paulo	Parana dominion	[5]
L. flavifrenatus	-23.66	-46.58	749	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.62	-46.55	750	Brazil, São Paulo	Parana dominion	[6]
L. flavifrenatus	-23.55	-46.64	758	Brazil, São Paulo	Parana dominion	[5]
L. flavifrenatus	-23.7	-46.7	767	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.53	-46.44	771	Brazil, São Paulo	Parana dominion	IBSP
L. flavifrenatus	-23.54	-46.47	771	Brazil, São Paulo	Parana dominion	[6]
L. flavifrenatus	-24.07	-54.31	262	Paraguay, Canindeyú	Parana dominion	[6]
L. flavifrenatus	-27.32	-56.58	78	Paraguay, Itapúa	Chacoan dominion	UNNEC
L. flavifrenatus	-27.12	-56.77	116	Paraguay, Misiones	Chacoan dominion	[10]
L. flavifrenatus	-24.5	-56.68	129	Paraguay, San Pedro	Parana dominion	[11]
L. flavifrenatus	-30.54	-57.86	37	Uruguay, Artigas	Chacoan dominion	[12]
L. flavifrenatus	-30.54	-57.83	42	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-30.35	-57.6	43	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-30.38	-57.63	43	Uruguay, Artigas	Chacoan dominion	[12]
L. flavifrenatus	-30.5	-57.83	44	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-30.39	-57.63	58	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-30.3	-57.6	62	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-30.3	-57.59	67	Uruguay, Artigas	Chacoan dominion	[13]
L. flavifrenatus	-31.68	-57.92	32	Uruguay, Paysandú	Chacoan dominion	[12]
L. flavifrenatus	-31.57	-57.93	45	Uruguay, Paysandú	Chacoan dominion	[12]
L. flavifrenatus	-31.58	-57.81	58	Uruguay, Paysandú	Chacoan dominion	[13]
L. flavifrenatus	-32.09	-57.56	60	Uruguay, Paysandú	Chacoan dominion	[13]
L. flavifrenatus	-31.58	-57.87	75	Uruguay, Paysandú	Chacoan dominion	[13]
L. flavifrenatus	-31.93	-57.57	108	Uruguay, Paysandú	Chacoan dominion	[13]
L. flavifrenatus	-31.69	-57.76	111	Uruguay, Paysandú	Chacoan dominion	[13]
L. flavifrenatus	-30.89	-57.75	34	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-30.94	-57.79	35	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-31.22	-57.82	42	Uruguay, Salto	Chacoan dominion	[13]

L. flavifrenatus	-31.04	-57.85	42	Uruguay, Salto	Chacoan dominion	[3]
L. flavifrenatus	-30.96	-57.8	44	Uruguay, Salto	Chacoan dominion	[12]
L. flavifrenatus	-31.52	-57.73	61	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-31.5	-57.73	63	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-31.27	-57.83	69	Uruguay, Salto	Chacoan dominion	[12]
L. flavifrenatus	-31.2	-57.35	70	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-31.28	-57.35	87	Uruguay, Salto	Chacoan dominion	[13]
L. flavifrenatus	-31.15	-57.85	53	Uruguay, Salto	Chacoan dominion	[13]
L. meridionalis	-27.56	-58.86	52	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-27.51	-58.73	61	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-27.3	-58.23	62	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-27.75	-58.01	68	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-27.95	-58.09	74	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-28.06	-58.26	77	Argentina, Corrientes	Chacoan dominion	[1]
L. meridionalis	-26.28	-58.31	69	Argentina, Formosa	Chacoan dominion	[1]
L. meridionalis	-25.42	-58.21	72	Argentina, Formosa	Chacoan dominion	[1]
L. meridionalis	-27.28	-55.44	121	Argentina, Misiones	Parana dominion	[1]
L. meridionalis	-19.83	-63.83	1313	Bolivia, Chuquisaca	South Brazilian dominion	[2]
L. meridionalis	-13	-64.83	143	Bolivia, El Beni	South Brazilian dominion	[2]
L. meridionalis	-17.83	-64	149	Bolivia, Santa Cruz	South Brazilian dominion	[2]
L. meridionalis	-17	-64	245	Bolivia, Santa Cruz	South Brazilian dominion	[2]
L. meridionalis	-17.76	-60.77	272	Bolivia, Santa Cruz	Chacoan dominion	[2]
L. meridionalis	-17.83	-62	293	Bolivia, Santa Cruz	South Brazilian dominion	[2]
L. meridionalis	-7.52	-63.03	57	Brazil, Amazonas	South Brazilian dominion	[14]
L. meridionalis	-14.12	-44.68	584	Brazil, Bahia	Parana dominion	[15]
L. meridionalis	-15.72	-48.17	166	Brazil, Distrito Federal	Chacoan dominion	[16]
L. meridionalis	-19.15	-39.91	30	Brazil, Espírito Santo	Parana dominion	[17]
L. meridionalis	-14.83	-49	545	Brazil, Goiás	Chacoan dominion	[2]
L. meridionalis	-18.79	-52.37	632	Brazil, Goiás	Chacoan dominion	[18]
L. meridionalis	-14.07	-47.38	780	Brazil, Goiás	Chacoan dominion	[19]
L. meridionalis	-18.33	-53	827	Brazil, Goiás	Chacoan dominion	[20]
L. meridionalis	-16	-57	172	Brazil, Mato Grosso	Chacoan dominion	[2]

L. meridionalis	-9.83	-55	283	Brazil, Mato Grosso	South Brazilian dominion	[2]
L. meridionalis	-15	-52	284	Brazil, Mato Grosso	Chacoan dominion	[2]
L. meridionalis	-13	-58.83	424	Brazil, Mato Grosso	Chacoan dominion	[2]
L. meridionalis	-17.31	-53.94	661	Brazil, Mato Grosso	Chacoan dominion	This study
L. meridionalis	-18.97	-56.61	105	Brazil, Mato Grosso do Sul	South Brazilian dominion	This study
L. meridionalis	-21.5	-57.57	132	Brazil, Mato Grosso do Sul	Chacoan dominion	This study
L. meridionalis	-20.47	-55.787	154	Brazil, Mato Grosso do Sul	Chacoan dominion	ZUFMS
L. meridionalis	-20.48	-55.81	160	Brazil, Mato Grosso do Sul	Chacoan dominion	ZUFMS
L. meridionalis	-21.15	-55.83	187	Brazil, Mato Grosso do Sul	Chacoan dominion	ZUFMS
L. meridionalis	-20.54	-56.71	238	Brazil, Mato Grosso do Sul	Chacoan dominion	ZUFMS
L. meridionalis	-21.45	-56.43	285	Brazil, Mato Grosso do Sul	Chacoan dominion	[21]
L. meridionalis	-23	-54	292	Brazil, Mato Grosso do Sul	Parana dominion	[2]
L. meridionalis	-20.83	-52	394	Brazil, Mato Grosso do Sul	Chacoan dominion	[2]
L. meridionalis	-21	-53	440	Brazil, Mato Grosso do Sul	Chacoan dominion	[2]
L. meridionalis	-20.93	-54.97	489	Brazil, Mato Grosso do Sul	Chacoan dominion	ZUFMS
L. meridionalis	-20	-48.83	593	Brazil, Minas Gerais	Chacoan dominion	[2]
L. meridionalis	-19	-48.83	729	Brazil, Minas Gerais	Chacoan dominion	[2]
L. meridionalis	-0.98	-49.73	19	Brazil, Pará	Boreal Brazilian dominion	[22]
L. meridionalis	-8.25	-49.28	172	Brazil, Pará	South-eastern Amazonian dominion	[23]
L. meridionalis	-8.25	-49.28	172	Brazil, Pará	South-eastern Amazonian dominion	[14]
L. meridionalis	-25.77	-49.72	924	Brazil, Paraná	Parana dominion	[24]
L. meridionalis	-25	-49	940	Brazil, Paraná	Parana dominion	[2]
L. meridionalis	-22	-51	408	Brazil, São Paulo	Parana dominion	[2]
L. meridionalis	-22.83	-48	483	Brazil, São Paulo	Chacoan dominion	[2]
L. meridionalis	-22.46	-48.98	551	Brazil, São Paulo	Chacoan dominion	IBSP
L. meridionalis	-21	-49	567	Brazil, São Paulo	Parana dominion	[2]
L. meridionalis	-20.83	-48	575	Brazil, São Paulo	Chacoan dominion	[2]
L. meridionalis	-23.49	-48.41	605	Brazil, São Paulo	Parana dominion	IBSP
L. meridionalis	-22.28	-48.13	645	Brazil, São Paulo	Chacoan dominion	IBSP
L. meridionalis	-21.78	-48.18	686	Brazil, São Paulo	Chacoan dominion	IBSP

L. meridionalis	-24	-49	710	Brazil, São Paulo	Parana dominion	[2]
L. meridionalis	-22.15	-47.83	734	Brazil, São Paulo	Chacoan dominion	[25]
L. meridionalis	-24.02	-47.92	808	Brazil, São Paulo	Parana dominion	[26]
L. meridionalis	-24.1	-48.03	839	Brazil, São Paulo	Parana dominion	[26]
L. meridionalis	-10.4	-46.7	425	Brazil, Tocantins	Chacoan dominion	[27]
L. meridionalis	-22.83	-56	298	Paraguay, Amambay	Parana dominion	[2]
L. meridionalis	-27.27	-56.1	75	Paraguay, Itapúa	Parana dominion	[1]
L. meridionalis	-27.29	-56.54	79	Paraguay, Itapúa	Chacoan dominion	[28]
L. meridionalis	-27	-56	117	Paraguay, Itapúa	Parana dominion	[2]
L. meridionalis	-27.25	-55.78	189	Paraguay, Itapúa	Parana dominion	[1]
L. meridionalis	-27.03	-56.69	141	Paraguay, Misiones	Chacoan dominion	[29]
L. meridionalis	-26.89	-58.34	57	Paraguay, Ñeembucú	Chacoan dominion	[1]
L. meridionalis	-24.58	-57.32	69	Paraguay, Presidente Hayes	Chacoan dominion	[30]
L. meridionalis	-23	-57.83	80	Paraguay, Presidente Hayes	Chacoan dominion	[2]
L. meridionalis	-23.8	-56.28	201	Paraguay, San Pedro	Parana dominion	[31]
L. paucidens	-23.8	-56.29	210	Paraguay, San Pedro	Parana dominion	[32]
L. paucidens	-17.72	-48.16	793	Brazil, Goiás	Chacoan dominion	[5]
L. paucidens	-17.72	-48.15	817	Brazil, Goiás	Chacoan dominion	[33]
L. paucidens	-17.67	-53.22	838	Brazil, Goiás	Chacoan dominion	[34]
L. paucidens	-17.32	-53.2	694	Brazil, Goiás	Chacoan dominion	[34]
L. paucidens	-15.95	-44.8667	461	Brazil, Minas Gerais	Parana dominion	[34]
L. paucidens	-15.91	-46.12	524	Brazil, Minas Gerais	Chacoan dominion	[34]
L. paucidens	-15.78	-48.7667	1161	Brazil, Goiás	Chacoan dominion	[33]
L. paucidens	-15.78	-47.93	1139	Brazil, Distrito Federal	Chacoan dominion	[35]
L. paucidens	-15.78	-48.77	1161	Brazil, Goiás	Chacoan dominion	[33]
L. paucidens	-15.71	-48.0224	1123	Brazil, Distrito Federal	Chacoan dominion	[33]
L. paucidens	-15.58	-56.0833	226	Brazil, Mato Grosso	Chacoan dominion	[34]
L. paucidens	-15.43	-55.75	613	Brazil, Mato Grosso	Chacoan dominion	[34]
L. paucidens	-15.33	-56.55	229	Brazil, Mato Grosso	Chacoan dominion	[34]
L. paucidens	-15.3	-55.85	640	Brazil, Mato Grosso	Chacoan dominion	[33]
L. paucidens	-15.29	-59.0608	324	Brazil, Mato Grosso	South Brazilian dominion	[33]
L. paucidens	-15.2	-45.8333	765	Brazil, Minas Gerais	Chacoan dominion	[34]

L. paucidens	-14.87	-55.7856	270	Brazil, Mato Grosso	Chacoan dominion	[33]
L. paucidens	-14.54	-40.3786	773	Brazil, Bahia	Parana dominion	[36]
L. paucidens	-14.08	-47.6167	1302	Brazil, Goiás	Chacoan dominion	[34]
L. paucidens	-14.07	-45.4333	742	Brazil, Bahia	Chacoan dominion	[33]
L. paucidens	-14.05	-48.3167	443	Brazil, Goiás	Chacoan dominion	[34]
L. paucidens	-14.03	-45.4519	726	Brazil, Bahia	Chacoan dominion	[33]
L. paucidens	-13.65	-51.15	227	Brazil, Mato Grosso	Chacoan dominion	[5]
L. paucidens	-13.62	-44.43	492	Brazil, Bahia	Parana dominion	[36]
L. paucidens	-13.55	-46.35	739	Brazil, Goiás	Chacoan dominion	[34]
L. paucidens	-12.6	-47.8667	292	Brazil, Tocantins	Chacoan dominion	[33]
L. paucidens	-12.57	-47.88	293	Brazil, Tocantins	Chacoan dominion	[37]
L. paucidens	-11.75	-50.7333	191	Brazil, Mato Grosso	Chacoan dominion	[33]
L. paucidens	-11.62	-50.6714	191	Brazil, Mato Grosso	Chacoan dominion	[34]
L. paucidens	-11.43	-42.5	1098	Brazil, Bahia	Chacoan dominion	[36]
L. paucidens	-11.22	-50.67	181	Brazil, Mato Grosso	Chacoan dominion	[5]
L. paucidens	-11.22	-50.6667	181	Brazil, Mato Grosso	Chacoan dominion	[33]
L. paucidens	-11.06	-42.4319	479	Brazil, Bahia	Chacoan dominion	[34]
L. paucidens	-10.74	-46.79	488	Brazil, Tocantins	Chacoan dominion	[34]
L. paucidens	-10.63	-46.6667	480	Brazil, Tocantins	Chacoan dominion	[34]
L. paucidens	-10.6	-46.81	470	Brazil, Tocantins	Chacoan dominion	[34]
L. paucidens	-10.3	-48.35	233	Brazil, Tocantins	Chacoan dominion	[34]
L. paucidens	-8.883	-44.9667	315	Brazil, Piauí	Chacoan dominion	[38]
L. paucidens	-8.833	-48.5	272	Brazil, Tocantins	Chacoan dominion	[34]
L. paucidens	-8.62	-48.32	265	Brazil, Tocantins	Chacoan dominion	[37]
L. paucidens	-5.57	-46.74	279	Brazil, Maranhão	Chacoan dominion	[39]
L. paucidens	-5.36	-42.85	72	Brazil, Maranhão	Boreal Brazilian dominion	[40]
L. paucidens	-5.32	-41.55	245	Brazil, Piauí	Boreal Brazilian dominion	[41]
L. paucidens	-5.083	-42.8	89	Brazil, Piauí	Boreal Brazilian dominion	[5]
L. paucidens	-4.65	-42.35	112	Brazil, Piauí	Boreal Brazilian dominion	[42]
L. paucidens	-4.11	-41.71	203	Brazil, Piauí	Boreal Brazilian dominion	[34]
L. paucidens	-4.106	-41.71	203	Brazil, Piauí	Boreal Brazilian dominion	[33]
L. paucidens	-3.28	-39.27	31	Brazil, Ceará	Chacoan dominion	[43]

L. paucidens	-2.9	-41.78	5	Brazil, Piauí	Boreal Brazilian dominion	[44]

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Table 2.S1. Summary of the selected variables to *Lygophis* species.

Type	Variable abbreviation	Brief description	Selected variables			
			L. dilepis	***L. flavifrenatus***	***L. meridionalis***	***L. paucidens***
Enrivonmental	BIO1	Annual Mean Temperature				
	BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	x		x	x
	BIO3	Isothermality (BIO2/BIO7) (×100)		x	x	x
	BIO4	Temperature Seasonality (standard deviation ×100)				x
	BIO5	Max Temperature of Warmest Month				
	BIO6	Min Temperature of Coldest Month		x		
	BIO7	Temperature Annual Range (BIO5-BIO6)				
	BIO8	Mean Temperature of Wettest Quarter	x	x	x	x
	BIO9	Mean Temperature of Driest Quarter		x		
	BIO10	Mean Temperature of Warmest Quarter				
	BIO11	Mean Temperature of Coldest Quarter				
	BIO12	Annual Precipitation	x	x	x	
	BIO13	Precipitation of Wettest Month				x
	BIO14	Precipitation of Driest Month			x	
	BIO15	Precipitation Seasonality (Coefficient of Variation)	x			
	BIO16	Precipitation of Wettest Quarter				
	BIO17	Precipitation of Driest Quarter				
	BIO18	Precipitation of Warmest Quarter		x	x	x
	BIO19	Precipitation of Coldest Quarter	x		x	x
Landscape	Coefficient of variation	Normalized dispersion of EVI	x	x		x
	Evenness	Evenness of EVI	x	x	x	x
	Range	Range of EVI	x	x	x	
	Shannon	Diversity of EVI				
	Simpson	Diversity of EVI				

	Standard deviation	Dispersion of EVI				
Topographic	Elevation	Elevation	x			x
	Slope	Average slope	x	x	x	x
	Aspect	Average aspect	x	x	x	x
Edaphic	Sand	Fraction of Sand				