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Original article

Distribution patterns of *Serjania* (Sapindaceae, Paullinieae) in Bolivia: a starting point for understanding its biogeographical history in America

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ABSTRACT

Serjania is the largest genus of Sapindaceae in the Americas; however, studies on its distribution are lacking. Current knowledge is based largely on the distribution pattern of the genus in Brazil, suggesting that species in wet areas have wider distributions than those in open or drier ones. Additionally, species in drier zones have been found to occur in various ecosystems, indicating niche specialization to resist hydric stress. In this study, we aimed to update the distribution pattern information for *Serjania* using Bolivia as a reference due to its diverse environmental conditions. We estimated species richness, identified environmental factors influencing species distribution, and created niche models. Our results confirm the previous hypotheses proposed by Acevedo-Rodríguez. We found that species occurring in dry zones are present in several ecosystems, all of which are Seasonally Dry Tropical Forests that are adapted to narrow ranges of temperature and rainfall regimes. Furthermore, our current and future projections show that the distribution of *Serjania* in South American Seasonally Dry Tropical Forests will become more interconnected. Our study highlights the importance of understanding the distribution of *Serjania* and its ecological requirements for its conservation and management in the future.

Keywords: Chiquitano dry forest, Niche modelling, Sapindaceae, Seasonally Dry Tropical Forest, Yungas slopes.

Introduction

Serjania Mill. according to Radlkofer (1931-1934), and as recently supported by Buerki *et al*. (2021), belongs to the Paullinieae tribe and is the largest genus of Sapindaceae in the New World, comprising approximately 240 species (Ferrucci & Steinmann 2019). The species of this genus are characterized by their climbing shrub or subshrub habit (lianas) and by the presence of schizocarpic fruits with three samaroid mericarps that have the locule in the distal portion. Its distribution ranges from southwestern United States to central Argentina, with Brazil, Mexico, and Bolivia being the major centers of diversity (Coulleri 2015). Bolivia harbors 58 species, which represents 25% of the total species of the genus (Coulleri 2015). Furthermore, all of them belong to the 12 sections recognized by Radlkofer (1931-1934) and

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the 6 ones proposed by Acevedo-Rodríguez (1993) *sensu* Coulleri and Ferrucci (2015).

Although *Serjania* is the most numerous genus in the Americas, only the Acevedo-Rodríguez (1990) Brazilian distribution analysis is available. According to this research, the species of *Serjania* are mainly distributed at a medium geographical range in the Americas, covering a quarter to a third of the continent's area. Around 35% of the species occupy a restricted range, which is usually endemic or narrowly endemic, probably adapted to open and drier areas. The remaining 5% are widespread species that occur in wetter regions than those occurring in drier areas. For his analysis, Acevedo-Rodríguez divided the occurrence of *Serjania* species into three regions originally proposed by Rizzini (1963): Amazon basin, Central planalto, and Atlantic coast.

Bolivia's forests are renowned for their incredible diversity of flora and fauna, containing more than 20,000 species of seed plants (Moraes & Beck 1992), 1274 bird species (Armonía 1995), and approximately 316 mammal species (Ergueta & Sarmiento 1992). According to Morrone's (2006) classification, Bolivia is represented by three biogeographic regions: the Amazon region (Yungas and Pantanal subregions), the Chaco region (Chaco subregion), and the South American transition zone (Puna and Atacama subregions). However, for the purposes of this work, the phytogeographical regions proposed by Killeen *et al.* (1993) are more relevant and accurate (Fig 1).

Killeen *et al.* (1993) proposed that in Bolivia are merged four phytogeographical regions of South America: Andes, Amazonia, Cerrado, and Gran Chaco, with a total of 13 vegetation types that can be divided according to climate, altitude, and geomorphology criteria. The Bolivian Amazon contains three formations: Amazon Forest, moist lowland forests, and moist forest of the Precambrian Shield. The Cerrado phytogeographical region has two formations: the savannas of the Cerrado fields and the Chiquitano dry forest. The Great Chaco consists of the Chaco dry forest of the plains and the Chaco Mountain Forest of the Andean foothills. The Andean region is divided into subregions based on altitude and the associated environmental changes. In the south of the country, the Tucumano-boliviano forest is located on the eastern ridges, while the Inter-Andean dry valleys are located in the area of vestigial rain to the west. To the north, the moist mountain forest is located in the Yungas of La Paz, Cochabamba, and Santa Cruz, and the Yungas Forest occurs at higher altitudes. The Altiplano, western

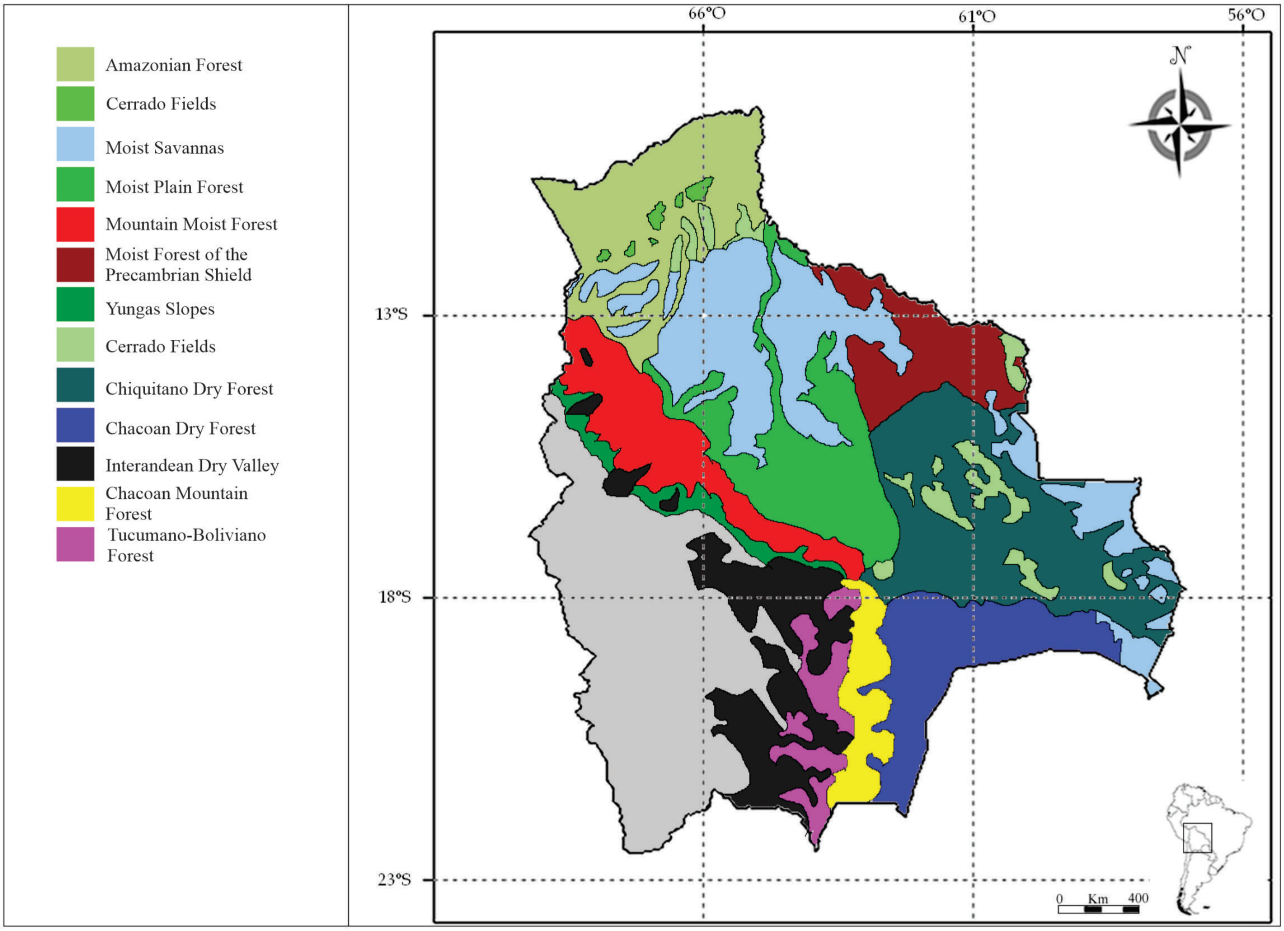


Figure 1. Bolivian vegetation types in accordance to Killeen *et al.* (1993).

lift, and part of the eastern mountains are characterized by Puna and high-Andean vegetation.

These forest formations are also present in other countries of South America. For instance, Cerrado fields, Chiquitano dry forest, and Amazon forests are present in Brazil, where the Chiquitano dry forest is known as Cerradão. Similarly, the wet savannas are shared with Venezuela, and the Yungas, Tucumano-boliviano forest, and the Chaco Forest are present in Argentina, where the latter is also in Paraguay. Bolivia, therefore, presents a transition between the most representative ecosystems of the South American continent.

To update the information about the *Serjania* genus, we estimated its species richness in Bolivia as a tool to achieve integrated knowledge of the distribution patterns of this genus. Additionally, we analyzed the richness maps through multiple regression and spatial analysis techniques in order to determine the environmental factors that influence species richness. Finally, by studying the present and future potential distribution in the American continent using bioclimatic variables, we determined the main ecosystems in which these plants grow.

Material and methods

Data collection and species richness estimation

Data on the distribution and environmental characteristics of *Serjania* species were collected from both the CTES Herbarium exsiccates and field trips. The latter consisted of 6 to 20 individuals per species and are listed in the Supplementary material.

To measure the diversity of *Serjania* species, we used species richness as an index. We estimated this index in the 13 Bolivian vegetation types by creating a 13 x 54 presence/absence matrix (refer to Table 1). The index was calculated using the following formula:

R = ni/N

where ni is the number of species in the i quadrant of the matrix, and N is the total number of species analyzed.

We also estimated the species richness index using the Richness function and the number of different classes as the output variable of the DIVA-GIS Software (Hijmans *et al*. 2005). This was done using a cell size of 1 x 1 and a simple point-to-grid procedure.

Table 1. Species distribution in relation to the Bolivian forest formation in which: AF (Amazonian forests), Yu (Yunga), ChF (Chiquitano Dry Forest), CDF (Chacoan dry Forest), MMF (Mountain moist forest), CF (Cerrado fields), TBF (Tucumano-Boliviano Forest), MS (Moist Savannas), MPF (Moist plain forest), PS (Moist forest of the precambrian shield), IDV (Interandean dry valleys), CMF (Chocoan mountain forest).

Species/Forest Formation	AF	Yu	ChF	CDF	MMF	CF	TBF	MS	MPF	PS	IDV	CMF	AmF
S. altissima	1	1	1	0	0	0	0	0	0	0	0	0	0
S. ampelopsis	0	1	1	1	0	0	0	0	0	0	0	0	0
S. atrolineata	0	0	1	0	0	0	0	0	0	0	0	0	0
S. caracasana	0	1	1	1	1	1	0	0	0	0	0	0	0
S. chacoensis	0	0	1	0	0	0	0	0	0	0	0	0	0
S. chaetocarpa	0	0	1	1	0	0	0	0	0	0	0	0	0
S. circumvallata	0	1	0	0	0	0	0	0	0	0	0	0	0
S. comata	0	1	1	0	0	0	0	0	0	0	0	0	0
S. communis	0	1	0	0	0	0	0	0	0	0	0	0	0
S. confertiflora	0	0	1	1	1	0	0	0	0	0	0	0	0
S. crassifolia	0	1	1	0	1	1	0	0	0	0	0	0	0
S. deltoidea	0	1	0	0	1	0	0	0	0	0	0	0	0
S. dibotrya	0	0	0	1	1	0	0	0	0	0	0	0	0
S. didymadenia	0	1	0	0	1	0	0	0	0	0	0	0	0
S. diffusa	0	0	0	0	0	0	1	0	0	0	0	0	0
S. dumicola	0	1	0	0	0	0	0	0	0	0	0	0	0
S. elongata	0	0	0	0	1	0	0	0	0	0	0	0	0
S. erecta	0	0	0	0	0	1	0	0	0	0	0	0	0
S. foveata	0	1	0	0	0	0	0	0	1	0	0	0	0
S. fuscifolia	0	0	1	0	0	0	0	0	0	0	0	0	0
S. glabrata	1	1	1	1	1	1	1	1	1	1	1	1	1
S. grandiceps	1	0	0	0	0	0	0	0	0	0	0	0	1
S. hebecarpa	0	0	1	1	0	0	0	0	0	0	0	0	0

Table 1. Cont.

Species/Forest Formation	AF	Yu	ChF	CDF	MMF	CF	TBF	MS	MPF	PS	IDV	CMF	AmF
S. inflata	0	0	0	0	1	0	0	0	0	0	0	0	0
S. leptocarpa	0	1	0	0	0	0	0	0	0	0	0	0	0
S. lethalis	0	1	1	0	1	0	0	0	0	0	0	0	0
S. leucosepala	0	0	1	0	0	0	0	0	0	0	0	0	0
S. longistipula	0	1	1	0	1	0	0	0	0	0	0	0	0
S. mansiana	0	1	1	1	0	0	0	0	0	0	0	0	0
S. marginata	1	1	1	0	0	1	0	0	0	0	0	0	0
S. meridionalis	0	1	0	0	1	0	0	0	0	0	0	0	0
S. minutiflora	0	0	1	1	0	0	0	0	0	0	0	0	0
S. mucronulata	0	1	0	0	0	0	0	0	0	0	0	0	0
S. neei	0	0	1	0	0	0	0	0	0	0	0	0	0
S. noxia	0	0	1	0	0	0	0	0	0	0	0	0	1
S. nutans	0	1	0	0	1	0	0	0	0	0	0	0	0
S. orbicularis	0	0	1	0	0	0	0	0	0	0	0	0	0
S. ovalifolia	0	0	0	0	0	1	0	0	0	0	0	0	0
S. paludosa	0	0	1	0	0	0	0	0	0	0	0	0	0
S. pannifolia	1	1	1	0	0	0	0	0	0	0	0	0	0
S. paucidentata	0	0	1	0	1	0	0	0	0	0	0	0	0
S. perulacea	0	0	1	0	0	0	0	0	0	0	0	1	0
S. platycarpa	0	0	1	0	1	0	0	0	0	0	0	0	0
S. pyramidata	0	1	1	0	0	0	0	0	0	0	0	0	0
S. reticulata	0	0	1	0	1	0	0	0	0	0	0	0	0
S. rigida	0	0	0	0	0	0	0	0	0	0	1	0	0
S. rubicaulis	1	1	1	0	0	0	0	0	0	0	0	0	0
S. rubicunda	0	1	0	0	0	0	0	0	0	0	0	0	0
S. setigera	0	0	1	0	0	0	0	0	0	0	0	0	0
S. souzana	0	0	1	0	1	0	0	0	0	0	0	0	0
S. sphaerococca	0	1	1	0	1	0	0	0	0	0	0	0	0
S. subrotundifolia	0	0	1	0	1	0	0	0	0	0	0	0	0
S. sufferruginea	0	1	1	0	1	0	0	0	0	0	0	1	0
S. tenuifolia	0	0	0	0	0	0	0	0	1	0	0	0	1
S. tripleuria	0	0	1	1	0	0	0	0	0	0	0	0	0

*Estimation of environmental variables that determine the **Serjania** distribution*

To evaluate the influence of environmental conditions on the distribution of each species, we used regression-tree models (hereafter RT models; Breiman *et al*. 1984; De'ath & Fabricius 2000). These models are ideal for identifying important predictor variables in the presence of non-linear predictor-response relationships and high-order predictor interactions, which is often the case when predicting species distributions using environmental variables Vayssieres *et al.* (2000). We employed the number of specimens of each species per quadrat as the response variable. To ensure the accuracy of the results, we used 4882 quadrats with a size of 15m×15m each one, this matrix covers all the Bolivian geography, the choice of the quadrat size is arbitrary in order to reduce as much as possible the quadrats sizes. To ensure the accuracy of the results we also test quadrat sizes of 50m×50m and 100m×100m in the analysis to assess the robustness of the results.We obtained 19 bioclimatic variables from the WorldClim database (Hijmans & Elith 2013), which are listed in Table 1 of the supplementary material. These variables are derived from monthly temperature and rainfall values, with a spatial resolution of 2.5 arc-minutes (5 km^2). To reduce redundancy and avoid collinearity among variables, we used the variance inflation factor (Dormann *et al*. 2007) and the Collinearity Diagnostic available in SPSS for linear regression analysis. We excluded variables with a variance inflation factor greater than 3, as suggested by Zuur *et al*. (2010). As a result, we identified 10 non-redundant climatic variables for both present and future scenarios: BIO 1 (annual mean temperature), BIO 3 (isothermality), BIO 4 (temperature seasonality), BIO 7 (temperature annual range), BIO 8 (mean temperature of wettest quarter), BIO 12 (annual precipitation), BIO 13 (precipitation of wettest month), BIO 14 (precipitation of driest month), BIO 15 (precipitation seasonality), and BIO 19 (precipitation of coldest quarter).

We conducted the RT analysis using the R package 'tree' (Ripley 2016), which was modified to include spatiotemporal variables. To evaluate the importance of each variable, we converted the RTs to 'rpart' (Therneau *et al*. 2015) objects. We employed the 'leave-one-out cross-validation' (LOOCV) method, as described by Arlot and Celisse (2010), to ensure that the RTs were fitted to the data and variables accurately.

*Present and future potential distribution of **Serjania***

Ecological niche models (ENMs) were used to estimate the potential distribution of *Serjania* species using Maxent software (Phillips *et al*. 2006), following the procedure proposed by Mukherjee *et al*. (2011). The occurrence data of *Serjania* were partitioned into 10 cross-validation folds, with 70% of randomly selected points for model training and the remaining 30% for model evaluation. The accuracy of the ENMs was evaluated using both threshold-dependent and threshold-independent approaches. The binary predictions were obtained using the minimum training presence as the threshold value. Omission rate (OR) was calculated for corresponding test data points as the fraction of all predicted pixels (FPA) according to Phillips *et al*. (2006). The accuracy of the models was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) curve, which was measured as the average and standard deviation of the cross-validated replicate runs. The ROCR package in R v. 3.1.2 was used to evaluate the models because it has been shown to perform better than other model evaluation methods (Elith *et al*. 2006; Hernandez *et al*. 2006; Aguirre-Gutiérrez *et al*. 2013). We selected the models with the highest AUC and lowest average OR and FPA for final Maxent model building, with high accuracy and reasonable area of prediction expected according to Hosmer *et al*. (2000).

The ENMs were built using the 19 bioclimatic variables from the Worldclim database at a resolution of 30 seconds (Hijmans *et al*. 2005), which was sufficient to generate effective and efficient approximations of habitable environments sensu Bucklin *et al*. (2015). We also projected the future geographic distribution of *Serjania* species under the SSP585 fossil-fueled development scenario proposed by the CMIP6, based on the ACCESS-CM2 Global Circulation Model (GCM) for 2041–2060 (mid-century) obtained from Fick & Hijmans (2017) – Fig 1 & 2 of Supplementary material-. To avoid discarding any occurrence record, we used the minimum training presence threshold for both present and future in the final distribution.

We compared the area occupied by the genus and species in the present with that which will be occupied in the future to estimate changes in their distribution and explore whether the geographic range will expand, contract, or move in any direction or if any of the species will go extinct.

Results

As part of this study, we conducted an updated analysis of the area extension of certain species, specifically those cited by Acevedo-Rodríguez (1990) as endemic to Brazil. Among these species are: *S. chaetocarpa, S. circumvallata, S. cissoides, S. cuspidata, S. orbicularis, S. paludosa, S. perulacea, S. platycarpa,* and *S. setigera*, the last of which was detected in Bolivia by Coulleri and Ferrucci (2015).

Distribution Patterns and Climatic Determinants

The estimation of species richness in Bolivian vegetation types revealed that the Chiquitano dry forest had the highest species diversity, followed by the Yungas slopes (Fig. 2). In contrast, the Precambrian shield moist forest and wet savannas had the fewest number of species, with only *Serjania glabrata* found in both regions.

Among the 54 species analyzed, several were restricted to specific vegetation types. For example, *S. atrolineata* C. Wright, *S. chacoensis* Ferrucci & Acev.-Rodr., *S. fuscifolia* Radlk., *S. leucosepala* Radlk., *S. neei* Acev.-Rodr., *S. orbicularis* Radlk., *S. paludosa* Cambess., and *S. setigera* Radlk. were found only in the Chiquitano dry forest, while *S. circumvallata* Radlk., *S. communis* Cambess., *S. dumicola* Radlk., *S. leptocarpa* Radlk., and *S. mucronulata* Radlk. were limited to the Yungas slopes. *S. elongata* J.F. Macbr. and *S. inflata* Poepp. were restricted to the Moist Mountain Forest, *S. diffusa* Radlk. and *S. erecta* Radlk. were limited to the Cerrado Field, *S. ovalifolia* Radlk. was present in the Tucumano-Boliviano Forest, and *S. rigida* Radlk. was found in the Inter-Andean dry valleys.

Eight species, including *S. altissima* (Poepp.) Radlk., *S. caracasana* (Jacq.) Willd., *S. glabrata* Kunth*, *S. hebecarpa* Benth., *S. longistipula Radlk.*, *S. mansiana* Mart., *S. marginata* Casar., and *S. sufferruginea* Radlk. had a wide distribution across Bolivia and all vegetation types. The remaining 28 species were distributed in two to four vegetation types.

Based on the DIVA-GIS estimations of species richness, the Chiquitano dry forest in Santa Cruz department and the Yungas in La Paz department had the richest regions (Fig. 3). Both vegetation types are considered tropical dry forests according to Portillo-Quintero and Sánchez-Azofeifa (2010).

The best predictors for the presence of *Serjania* species were annual mean temperature, temperature annual range,

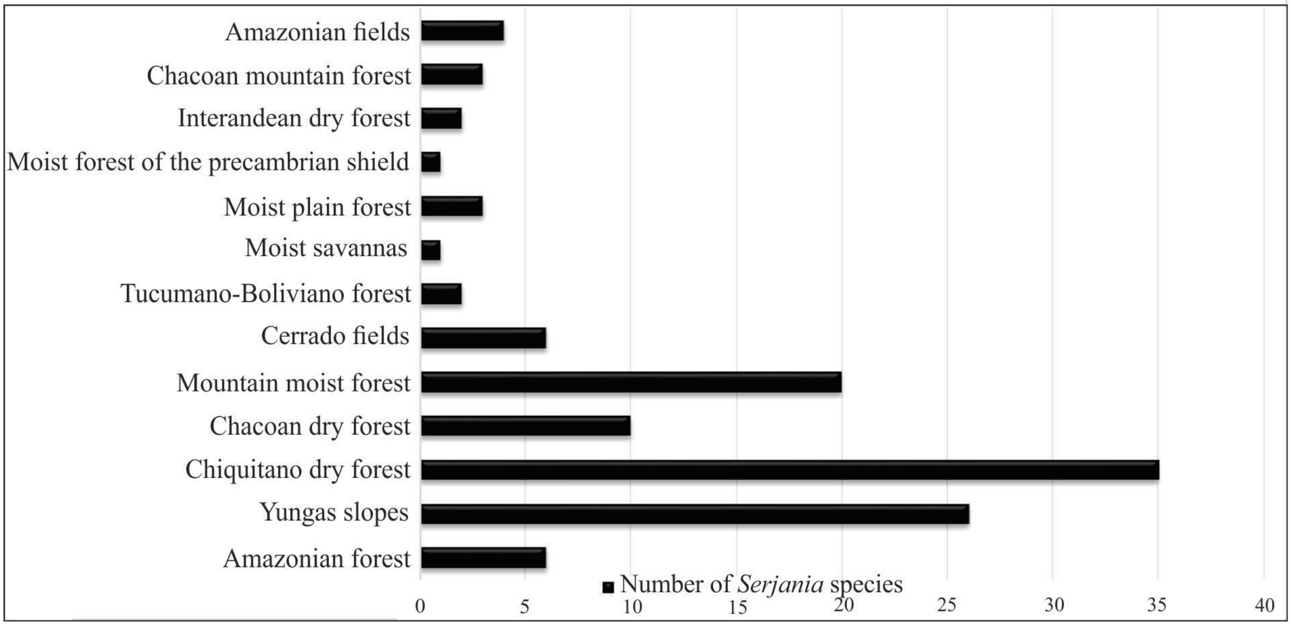


Figure 2. Number of *Serjania* species regarding to each Bolivian forest formation *sensu* Killeen *et al*. (1993) in which is remarkable the high number of it in the Chiquitano dry forest followed by the Yungas slopes.

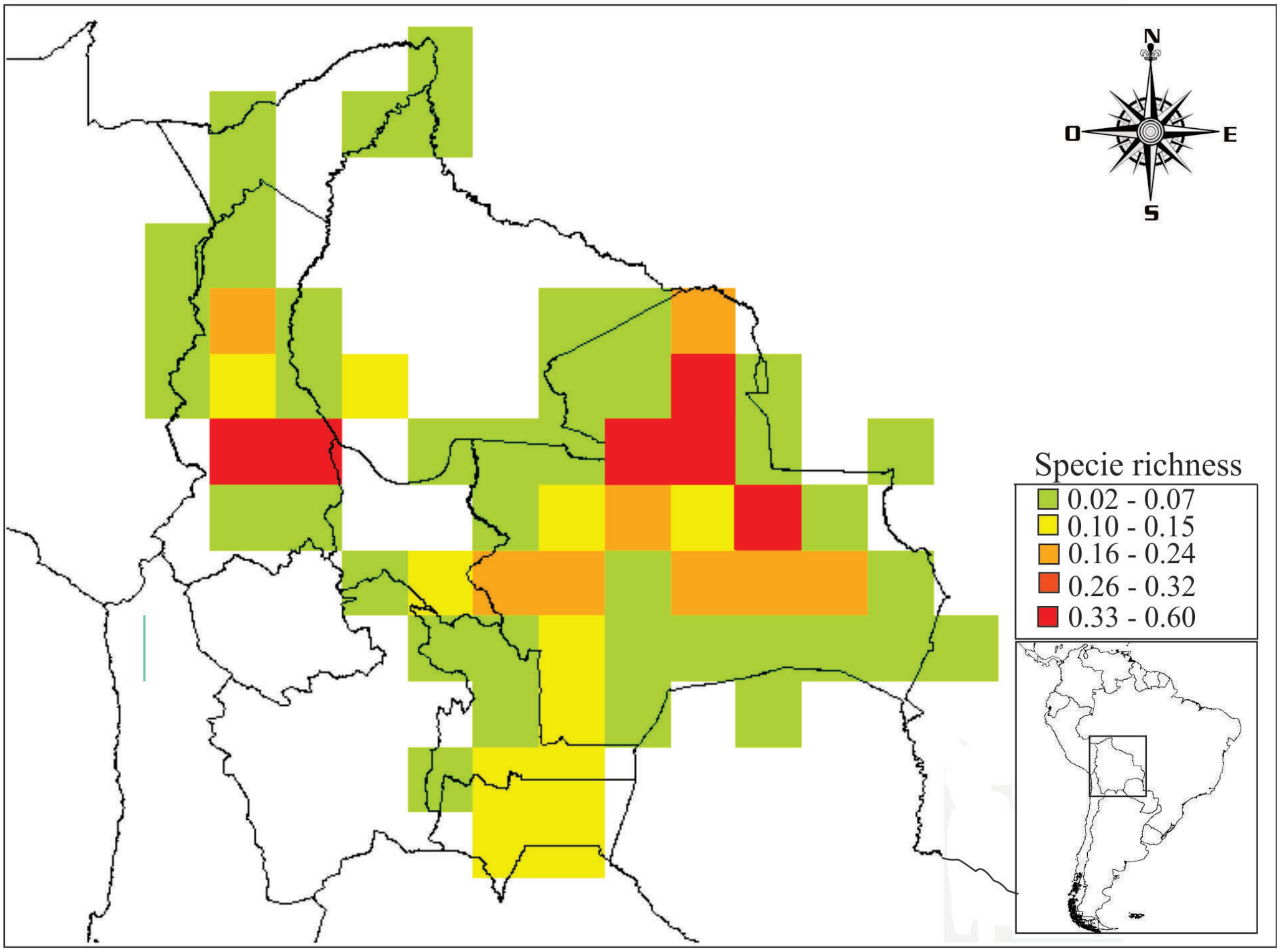
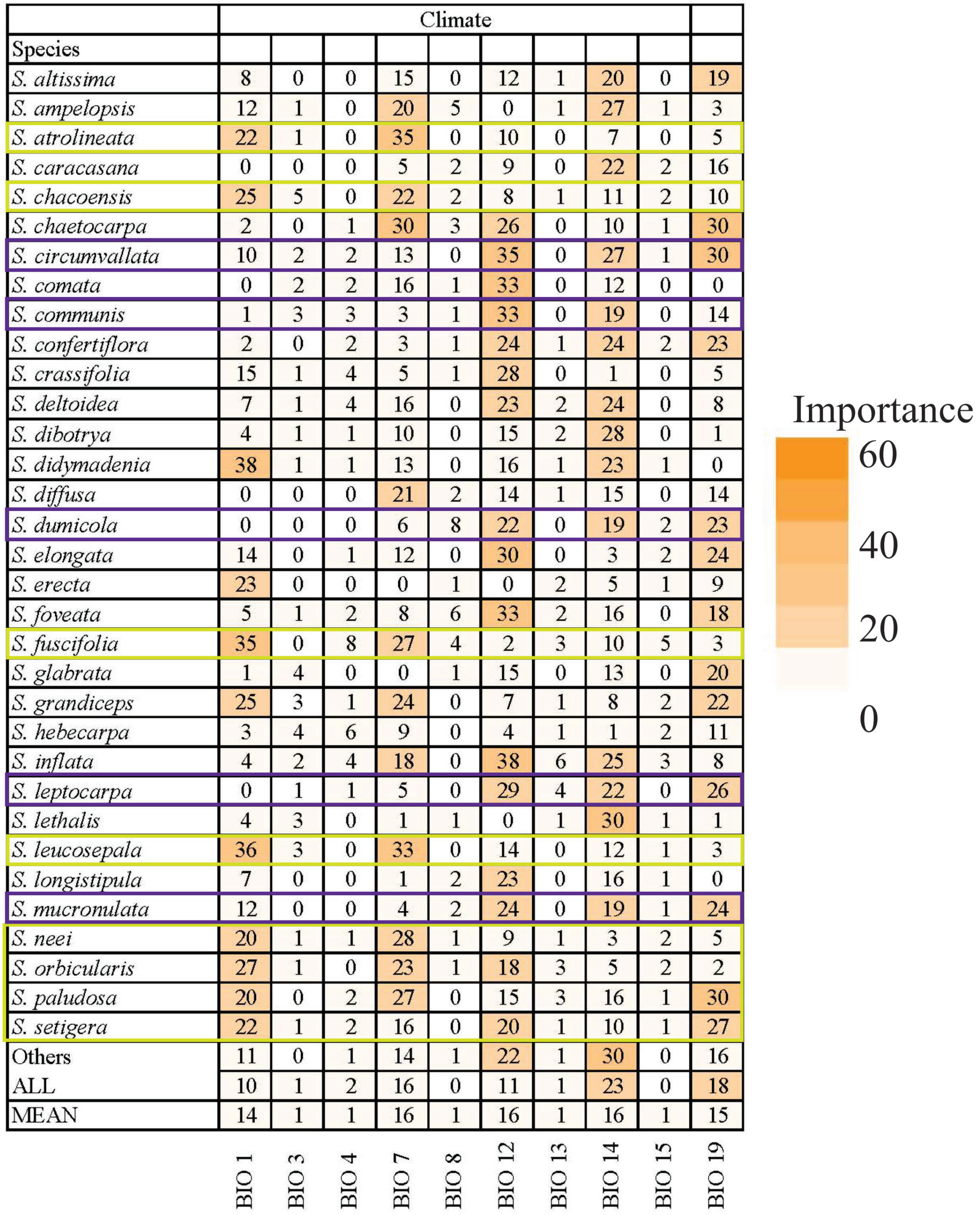


Figure 3. Species richness estimation of *Serjania*, the richest spots are located in La Paz and Santa Cruz departments. These spots coincide with the Yungas slopes and Chiquitano dry forest.

annual precipitation, precipitation of driest month, and precipitation of coldest quarter (Fig. 4). The mean residual spatial autocorrelation was 187 m, and the variogram did not show signs of leveling-off even at the maximum possible spatial lag of 500 m. Species in the Chiquitano dry forest were limited by a narrow temperature annual range, with most species unable to tolerate changes of more than 3°C above or below the range of 19°C to 33°C. Meanwhile, species in the Yungas were limited by annual precipitation, with a range of 2500 to 3500 mm.



	Climate									
Species										
S. altissima	8	0	0	15	0	12	1	20	0	19
S. ampelopsis	12	1	0	20	5	0	1	27	1	3
S. atrolineata	22	1	0	35	0	10	0	7	0	5
S. caracasana	0	0	0	5	2	9	0	22	2	16
S. chacoensis	25	5	0	22	2	8	1	11	2	10
S. chaetocarpa	2	0	1	30	3	26	0	10	1	30
S. circumvallata	10	2	2	13	0	35	0	27	1	30
S. comata	0	2	2	16	1	33	0	12	0	0
S. communis	1	3	3	3	1	33	0	19	0	14
S. confertiflora	2	0	2	3	1	24	1	24	2	23
S. crassifolia	15	1	4	5	1	28	0	1	0	5
S. deltoidea	7	1	4	16	0	23	2	24	0	8
S. dibotrya	4	1	1	10	0	15	2	28	0	1
S. didymadenia	38	1	1	13	0	16	1	23	1	0
S. diffusa	0	0	0	21	2	14	1	15	0	14
S. dumicola	0	0	0	6	8	22	0	19	2	23
S. elongata	14	0	1	12	0	30	0	3	2	24
S. erecta	23	0	0	0	1	0	2	5	1	9
S. foveata	5	1	2	8	6	33	2	16	0	18
S. fuscifolia	35	0	8	27	4	2	3	10	5	3
S. glabrata	1	4	0	0	1	15	0	13	0	20
S. grandiceps	25	3	1	24	0	7	1	8	2	22
S. hebecarpa	3	4	6	9	0	4	1	1	2	11
S. inflata	4	2	4	18	0	38	6	25	3	8
S. leptocarpa	0	1	1	5	0	29	4	22	0	26
S. lethalis	4	3	0	1	1	0	1	30	1	1
S. leucosepala	36	3	0	33	0	14	0	12	1	3
S. longistipula	7	0	0	1	2	23	0	16	1	0
S. mucronulata	12	0	0	4	2	24	0	19	1	24
S. neei	20	1	1	28	1	9	1	3	2	5
S. orbicularis	27	1	0	23	1	18	3	5	2	2
S. paludosa	20	0	2	27	0	15	3	16	1	30
S. setigera	22	1	2	16	0	20	1	10	1	27
Others	11	0	1	14	1	22	1	30	0	16
ALL	10	1	2	16	0	11	1	23	0	18
MEAN	14	1	1	16	1	16	1	16	1	15
	BIO 1	BIO 3	BIO 4	BIO 7	BIO 8	BIO 12	BIO 13	BIO 14	BIO 15	BIO 19

Figure 4. Variable importance for the presence of *Serjania* species. The variable importance scores signify of the fit resulting from the selection of a determined variable and the number of times that appear either as primary variable or as a surrogate one. Higher numbers explain mor of the variance of a predictor. All values are rounded. ALL represent all species in a plot pooled. In yellow are highlighted the species that only grows in the Chiquitano dry forest which presence is strong influenced by temperature variables, while in violet are remarked the species that inhabit only in the Yungas slopes in which the precipitations play an important role on their distribution.

Present and Future Potential Distribution of **Serjania**

The models produced showed strong predictive power, with AUC scores above 0.90 for both present and future scenarios. In addition, they presented low omission rate (OR) values ranging from 0.002 to 0.005 and FPA values ranging between 0.81 and 0.84.

Based on the data from Bolivia, the potential distribution of the *Serjania* genus in the American continent is illustrated in Fig. 5. Our predictive simulations identified possible richest regions in the Caatinga, Cerrado, and Chaco, which are consistent with the Amazon and Chaco subregions in the sense of Morrone (2006) (Fig. 6). These results support the hypothesis proposed by Ibisch (2005) that Bolivia serves as a South American ecotone.

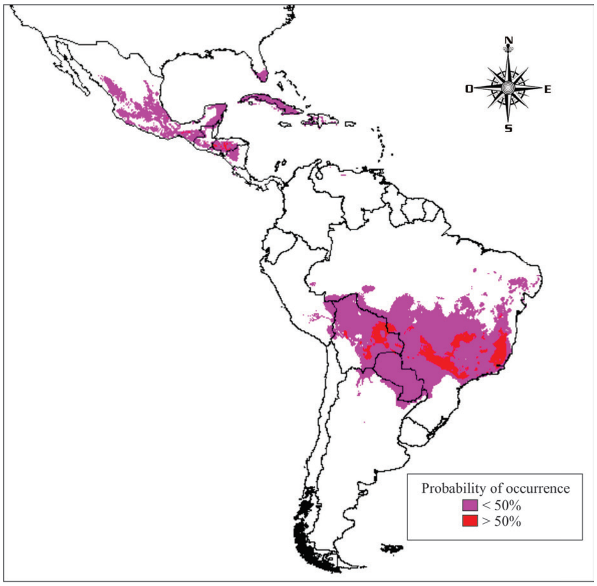


Figure 5. Projection of the present genus distribution in America based in the occurrence of *Serjania* in Bolivia.

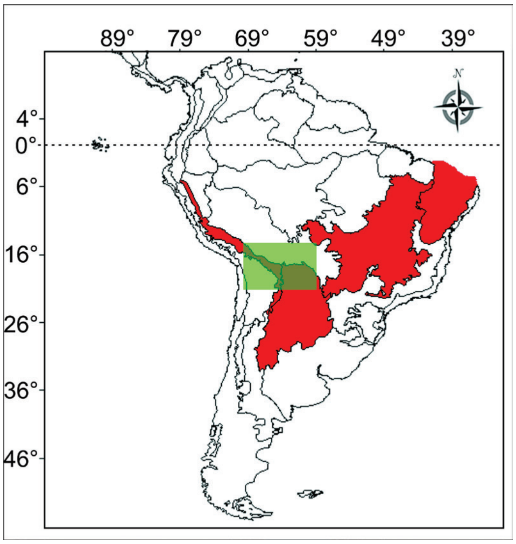


Figure 6. *Serjania* richness areas following the Morrone's (2006) biogeographical provinces, in Bolivia Yungas and Chaco provinces, green rectangle, and in Brazil Caatinga and Cerrado ones.

Figure 7 shows the future distribution of the genus and the change in occupied areas in the Americas relative to the selected scenario. According to our simulations, the distribution of 12 species will be reduced: *S. ampelopsis, S. atrolineata, S. crassifolia, S. deltoidea, S. erecta, S. inflata, S. lethalis* (Fig. 8 A, B), *S. longistipula, S. meridionalis* (Fig. 8 C, D), *S. pyramidata, S. reticulata,* and *S. sufferruginea,* and *S. tenuifolia* will disappear completely from Brazil. Conversely, *S. elongata, S. glabrata* (Fig. 9 A, B), *S. mansiana, S. marginata* (Fig. 9 C, D), and *S. sphaerococca* will extend their distribution patterns. Among these species, the most concerning case is *S. subrotundifolia*, which is predicted to go extinct between 2041 and 2060.

Discussion

The Paullinieae tribe is composed of six genera: *Cardiospermum* L., *Lophostigma* Radlk., *Paullinia* L., *Serjania* Mill., *Thinouia* Triana & Planch., and *Urvillea* Kunth. (Acevedo-Rodríguez *et al.* 2017). Together, these genera contain almost 500 neotropical species. Of these, *C. corindum* L., *C. halicacabum* L., and *P. pinnata* L. have widespread distribution, and *C. grandiflorum* Sw. is invasive in Africa, Asia, and Oceania (Coulleri *et al.* 2020).

Unlike *Cardiospermum* and *Urvillea*, which predominantly inhabit dry regions (Coulleri & Ferrucci 2012), or *Paullinia*, which is mostly found in humid areas (Medeiros *et al.* 2016), *Serjania* can be found in both wet and dry environments. However, as Acevedo-Rodríguez (1990) demonstrated, there is a slightly higher diversity of species in dry environments. This distribution pattern can be explained by the hypothesis that species in wet areas have a wider distribution than those in open or drier areas. Furthermore, distribution patterns in open and dry areas are due to physical barriers or ecological specialization, and the species in these zones occur in a vast number of ecosystems.

Our study partly agrees with Acevedo-Rodríguez's hypotheses. In Bolivia, the eight most widely distributed species, except for *S. glabrata*, are most representative of the Chiquitano dry forest, Chacoan dry forest, and Cerrado fields. These vegetation types are dry environments, so the hypothesis that species in wet areas have a wider distribution does not match our results. Perhaps this is due to the fact that in Brazil, the wetlands are drained by the Amazon River and its tributaries, which may be involved in the dispersal of the *Serjania* species, as mentioned by Acevedo-Rodríguez (1990).

In contrast, in Bolivia, the wet areas in which the widest species inhabit correspond to the Yungas slopes and Mountain moist forest, which are found on the eastern slopes of the Andes. Unlike the Brazilian wetland, the moisture in these regions is due to an annual rainfall regime above 2000 mm and the presence of orographic fog during most of the year. Moreover, mountain ranges with

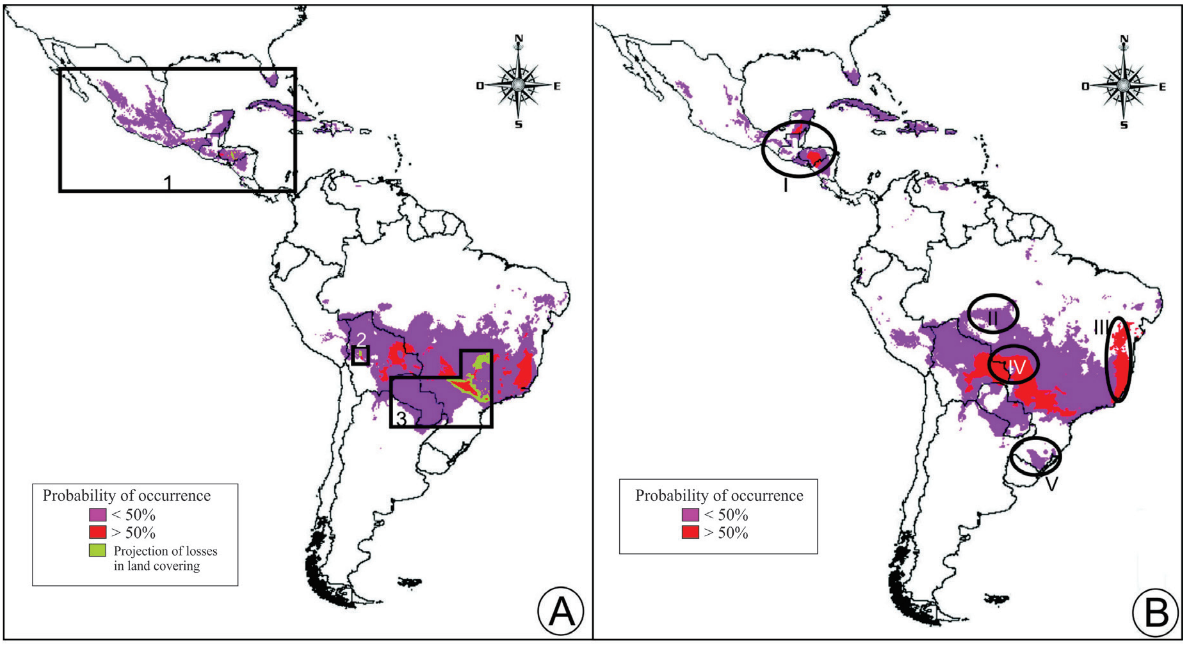


Figure 7. Present (**A**) and Future (**B**) distribution of *Serjania* in America regarding to the SSP585 scenario. In the current *Serjania* distribution (A) 1, 2, 3 represent the projected losses in land covering of some species in relation with the chosen future scenario. And, I, II, III, IV, V represent increase of the concentration of the species and land covering of some *Serjania* species in the SSP585 scenario.

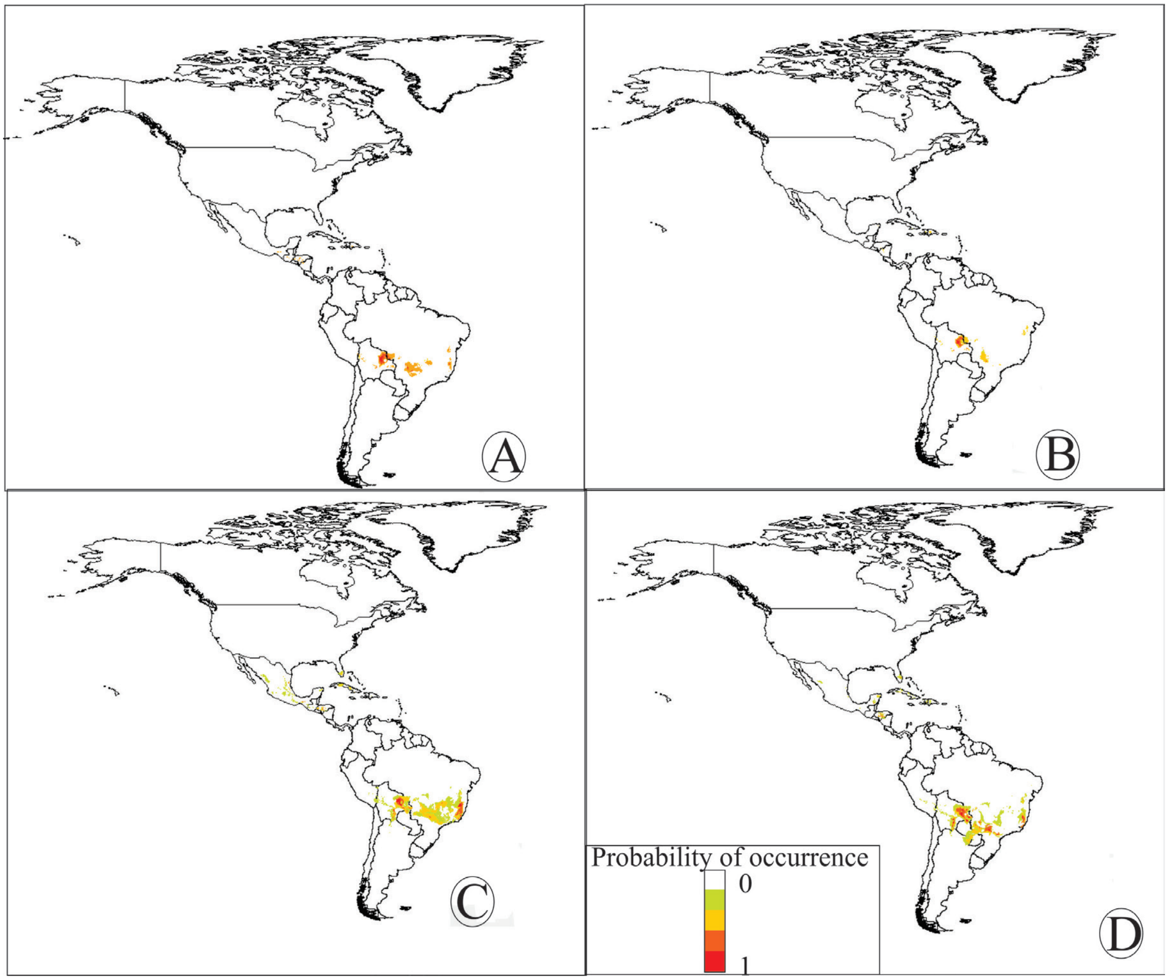


Figure 8. Distribution of *Serjania lethalis* in the present (**A**) and future (**B**); and *S. meridionalis* in present (**C**) and future (**D**).

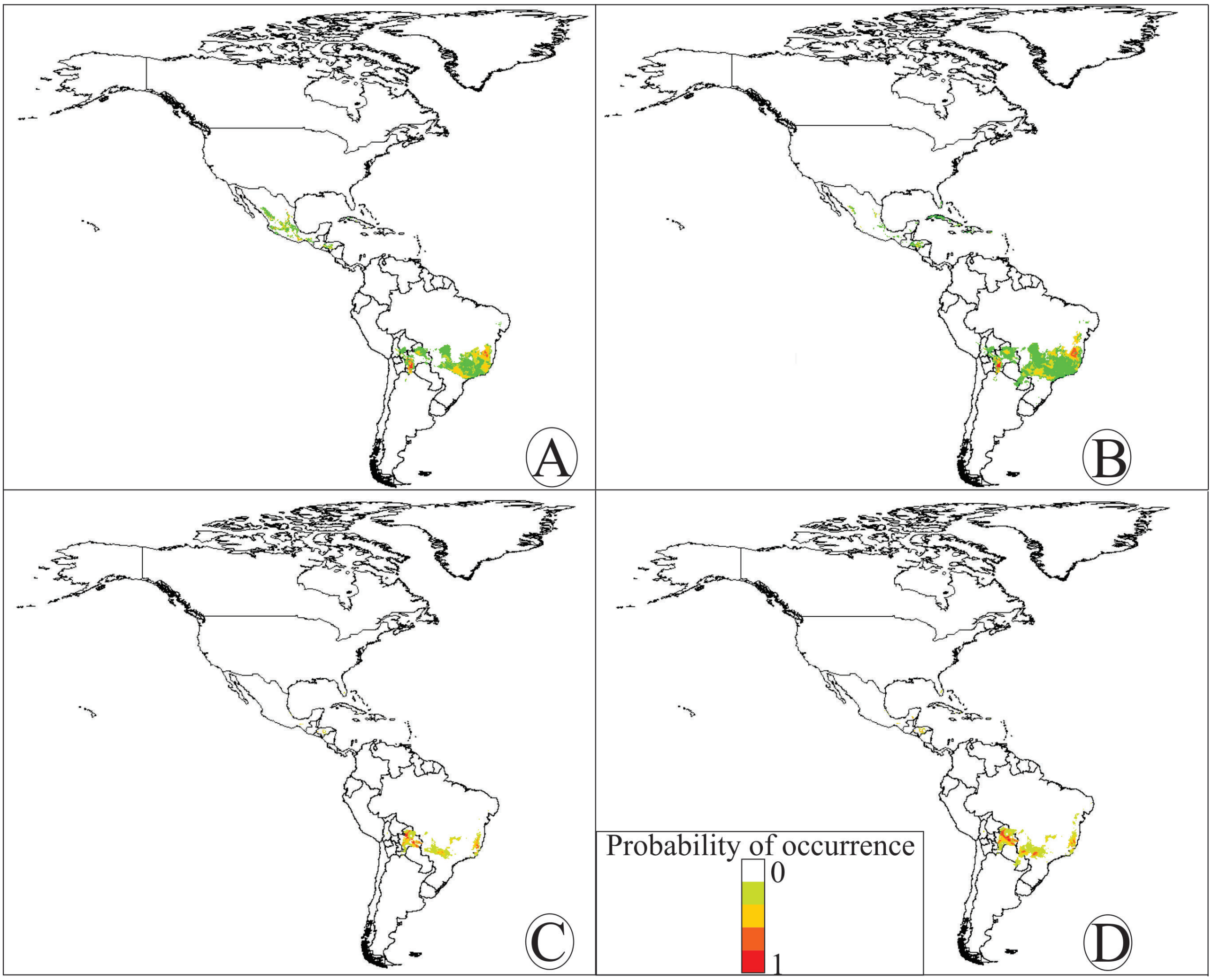


Figure 9. Distribution of *Serjania glabrata* in the present (**A**) and future (**B**); and *S. marginata* in present (**C**) and future (**D**).

hillocks and broad slopes, ravines, and narrow valleys are the geomorphological features of this region (Killeen *et al*. 1993), where no river would fulfill the function of dispersion as does the Amazon basin in Brazil.

According to our results, the Yungas slopes and Mountain moist forest are the second- and third-richest areas for *Serjania* species, while the Chiquitano dry forest, Chacoan dry forest, and Cerrado fields are the first, fourth, and fifth ones. This richness pattern is not surprising because these five vegetation types are neighbors and differentiate between wet and dry environments by rainfall regimes and altitude. In the case of the moist forest formation, the edaphic, floristic, and climatic conditions are similar between them (Killeen *et al*. 1993). However, in the dry ones, although they share some characteristics, each one has its particularities, and all of these environments are now considered as the seasonal dry tropical forest complex (SDTF) (Prado & Gibbs 1993; Prado 2000; Pennington *et al*. 2000; 2004), which agrees with Acevedo-Rodríguez's (1990) hypothesis that species that vegetate in dry areas occur in a vast number of ecosystems, which are all considered SDTF.

The Chiquitano dry forest has the highest concentration of *Serjania* species, among which are eight species that only occur in this forest formation. This ecosystem represents the largest extant patch of SDTF and is situated across a climatic transition between the humid evergreen forests of the Amazon and the deciduous thorn-scrub vegetation of the Gran Chaco.

To explain the high diversity of the Chiquitano dry forest, we must consider the mechanistic explanation for liana distribution and diversity among forests proposed by Schnitzer (2005; 2018) and DeWalt *et al*. (2010; 2015). They state that lianas grow particularly well during high light conditions and severe prolonged water stress, as during the 3-5 months of drought typical of the eastern lowland Bolivian forest. This dry season gives lianas an extended period of high growth each year, which is not evidenced in wet aseasonal forests. Lianas present a seasonal growth advantage (SGA) in relation to trees of dry environments or lianas that inhabit wetlands (Schnitzer 2005; 2018; Swaine & Grace 2007). This SGA could be explained by ecological, anatomical, and physiological adaptations of lianas. In the case of the species that grow exclusively in the Chiquitano dry forest, these adaptations are highly influenced by temperature changes that are expected in this kind of environment (Allen *et al*. 2017; Pulla *et al*. 2021). These *Serjania* species have extremely deep and efficient roots, and their vascular systems are comprised of a compound vascular cylinder consisting of three to ten slightly narrower vessels than other species of the genus (Coulleri 2015). This adaptation allows these species to tap water and nutrients that many trees and shrubs are unable to access during drought conditions, reducing the possibility of embolism.

Another adaptation that ensures vigorous growth during the hot and sunny conditions that are present during seasonal drought is a reduction in the leaf area, which is presented in the eight exclusively species of the Chiquitano dry forest (Coulleri 2015). Through this adaptation, the species that vegetate in this dry environment would minimize the trade-off between photosynthesis and water loss (Gleason *et al*. 2015; DeGuzman *et al*. 2017). This is crucial because lianas remain photosynthetically active during this season (Castellanos 1991; Zotz & Winter 1996). Another mechanism proposed by Schnitzer (2018) to minimize this safety trade-off is by operating at maximum photosynthesis earlier in the day. This 'fast and furious' strategy would allow lianas, when the ambient temperature is relatively low and the amount of water in the air is relatively high, to perform a high rate of photosynthesis with less water loss. At noon, when the temperatures increase, they close their stomata to prevent excess water loss. Lianas can maximize photosynthesis while preventing their xylem water tension from becoming dangerously negative.

Why the Chiquitano dry forest is richer than Chacoan dry forest and Cerrado fields, even though the latter are also dry environments, lies in the soil conditions. Chacoan dry forest and Cerrado fields present poor or shallow soils with a lateritic or bedrock layer in the subsoil or even salty soils (Killeen *et al*. 2005), while the Chiquitano dry forest has the most fertile soils and also better retains moisture (Dexter *et al*. 2018), which allows for the growth and maintenance of liana diversity (Schnitzer 2005).

In the wet environment of Yungas and Mountain moist forest, water is rarely scarce, while the rainfall regime is not altered. Light and soil nutrients are the limiting growth factors for lianas (Medina-Vega *et al*. 2021). Accordingly, the *Serjania* species that vegetate in these vegetation types present adaptations that allow them to compete with the characteristic tall trees of these environments. One of these adaptations is a leaf area that ranges from 21.15 cm to 97.53 cm (Coulleri 2015), this characteristic is also observed in trees that grows in this type of environment, even more so when the environments are stable and not of recent succession (Poorter & Arets 2003). Another is that all the species exclusive to the Yungas have wide vessels that make up a compound vascular system always with three peripheral cylinders and a central one (Coulleri 2015) for quick and efficient nutrient and water transport to the tall canopy on which the leaves should be arranged. This adaptation is possible because embolism in wet environments is less likely than in dry ones.

As for the present and future potential distribution of *Serjania*, the models performed well in predicting the current distribution of the studied *Serjania* species in the Americas. Therefore, our results confirm the hypothesis that Bolivia is a South American ecotone and that it harbors all the ecoregions of the continent. The potential distribution of the *Serjania* genus coincides with the current extent of the SDTFs, especially with those of central Brazil and Caatinga. The future projections for *Serjania* distribution suggest an increase in the SDTFs in southern areas of South America, which could be due to the increase in the maximum temperature expected by 2041-60 in accordance with the future scenario used in this analysis. These increments will lead to the connection of the Chiquitano dry forest with the Pantanal and the Cerrado of Brazil. Another phenomenon of ecosystem linkages could occur, according to our model, between the Mata Atlantica forest formation with the Caatinga. These tropical dry forest expansions would indicate a widespread reduction in precipitation across tropical South America, which would lead the SDTFs to occupy, in accordance to Prado (2000), their original geographical distribution, which dates back to the Last Glacial Maximum.

Conversely, the Caribbean *Serjania* populations show a decrease in land cover, with its distribution being concentrated in the current SDTFs of Mexico and Central America. The conversion of the SDTF to pasture and agriculture land has been a common practice in the region, and intact forests are now very scarce. Banda *et al*. (2016) claim that only 27% of the original SDTFs remains undisturbed in Mexico, with the remaining 73% having some degree of disturbance from alteration or degradation up to a total conversion of structure and function.

The distribution patterns of *Serjania* in Bolivia indicate that its species are more abundant in dry regions such as the SDTF in which they present better adapted traits and less competition between them and among other trees or shrubs than in moist environments. For the Americas, the SDTFs are candidates for presenting high diversity of *Serjania* species, especially the Atlantic Forest, the Cerrado, and the Chiquitano dry forest

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