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# Conservation Priorities for the Genus *Serjania* (Sapindaceae, Paullinieae), a Key Component in the Secondary Succession of the Seasonally Dry Tropical Forest in Bolivia

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#### **Research Article**

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# Abstract

Bolivia is a country with a huge environmental variety, most of which are classified as seasonally dry forest, these ecosystems are threatened due land use, then subsequent abandonment promote the regrowth of the forest by secondary succession. Therefore, identify species that lead this process is key in order to protect them, being lianas good candidates as it the *Serjania* genus. Our objectives were defining conservation priorities of *Serjania* species richness estimation; determine environmental factors that influence the distribution of these species and understand the dynamic of the SDTFs and secondary forest in America through present and future *Serjania* niche modelling. Our results set the conservation priorities in the Yungas slopes and the Chiquitano dry forest of Bolivia, these are the most diverse forests formations of the country, being the Chiquitano dry forest one of the most long-term stable American dry forests. Regarding to the environmental factors, for the species that only vegetate in the Chiquitano dry forest the temperature was the most important one, while the species that inhabit in the Yungas slope the precipitation regime represent the most influential variable for the presence of the species in these habitats. As for the dynamics of the Seasonally dry forest through *Serjania* distribution modelling, an increase in the land coverage by these ones at the expense of their neighboring wet forest is projected, which also indicate the progression of the secondary forest due land use and climate change.

## Introduction

Natural systems and their biodiversity provide a wide range of wealth and services to society, such as weather, water, and regulators of pollinators and dispersers; these services are essential for the wellness and development of human populations (Laterra et al. 2011).

The environments and their underlying processes could present different strategies to persist over time (Grime 2002, Vile et al. 2006). Some of these processes are important in terms of ecological successions (Bazzaz 1979, Huston and Smith 1987, Walker and del Moral 2003), such as those used by plants related to nutrient, water and light use, and the dispersal-regeneration strategies involving seed mass and seed output (Westoby et al. 2002, Dematteis et al. 2019, 2020).

The importance of secondary vegetation in tropical forests of the American continent has been studied for more than 40 years (Budowski 1961, Gómez-Pompa and Vásquez-Yanes 1974). However, many of these works have addressed moist forests (Brown and Lugo 1990, Finegan 1996, Guariguata and Ostertag 2001). Instead, comparatively few studies have focused on tropical dry forests of the Americas, although the latter occupy larger areas than moist forests, and their rate of conversion to secondary forests has been historically higher (Mooney et al. 1995).

Succession in the tropical dry forests of the Americas is poorly known and should be investigated. Bolivia is a country with a comparatively small territory but where all the environmental types of the continent are found, leading to a great environmental variation. Moreover, due to their great diversity and the increasing pressure from non-forest land uses, all the Bolivian forests could soon become a global conservation priority spot (Parker et al. 1993, Mooney et al. 1995, Dinerstein et al. 1995, Killeen et al. 1998). Therefore, recognizing species that initiate the secondary successional process is of great importance for conservation efforts. Lianas are possible candidates because these plants have been recognized as drivers of the reconstitution of treefall gaps in tropical and subtropical forests (Schnitzer and Bongers 2002). Lianas were also classified as early successional drivers in young secondary forests that have undergone large scale disturbances (Hegarty 1993, Troy et al. 1997, DeWalt et al. 2000).

According to Radlkofer (1931–1934), and recently supported by Buerki et al. (2021), the genus *Serjania* Mill. belongs to the Paullinieae tribe. This is the largest genus of Sapindaceae in the New World; it comprises ca. 240 species (Ferrucci and Steinmann 2019), with Brazil, Mexico and Bolivia being the major centers of diversity. 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. Bolivia harbors 58 species, which represents 25% of the total species of the genus (Coulleri 2015a); moreover; all the species belong to the 12 sections recognized by Radlkofer (1931–1934) and the 6 ones proposed by Acevedo-Rodríguez (1993) *sensu* Coulleri and Ferrucci (2015).

In the last decades, advances in Geographical Information Systems (GIS) have allowed us to model species' distributions based on environment attributes that are correlated with species' niche requirements (Guisan and Thuiller 2005, Peterson 2011). The models are overlapped to generate maps showing gradients of species richness, a fundamental metric of biodiversity in ecology and conservation planning (Ricklefs 2004).

The aims of this study were to: I) estimate *Serjania* species richness in Bolivia as a tool for conservation planning due to the importance of this genus in secondary succession; II) analyze the richness map through multiple regression and spatial analysis techniques in order to determine the environmental factors that influence species richness; III) to establish conservation hotspots of the tropical dry forest in the American continent by studying the present and future potential distribution in the American continent using bioclimatic variables.

# Material And Methods

### Bolivia as part of the South American transition zone, an ecotone

The Bolivian forests are not as diverse as the eastern forests of Peru and Ecuador, or as famous as the Brazilian Amazon. However, Bolivian forests contain one of the richest groups of flora and fauna in the world, with about 316 mammal species (Ergueta and Sarmiento 1992), 1274 bird species (Armonía 1995) and more than 20,000 species of seed plants (Moraes and Beck 1992). According to Morrone (2006), three biogeographic regions

are represented in Bolivia: the Amazon region (Yungas and Pantanal subregions); the Chaco region (Chaco subregion) and the South American transition zone (Puna and Atacama subregions). However, phytogeographically, the regions proposed by Killeen et al. (1993) are more accurate in relation to the objectives of this work (Fig 1).

Killeen et al. (1993) propose that four phytogeographical regions of South America are merged in Bolivia: Andes, Amazonia, Cerrado and Gran Chaco. Each region can be divided into various formations according to climate, altitude and geomorphology criteria, totaling 13 forest formations. Thus, the Bolivian Amazon comprises 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. Finally, 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 according to the 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 a higher altitude. The Altiplano, western lift and part of the eastern mountains are characterized by Puna and high-Andean vegetation.

Most of those forest formations also are present in other countries of South America. For example, Cerrado fields and Chiquitano dry forest and Amazon forests are present in Brazil. The Chiquitano dry forest in Brazil is called Cerradão. In turn, the wet savannas are shared with Venezuela, whereas the Yungas, Tucumano-boliviano forest, and the Chaco forest are also present in Argentina, and the latter is also in Paraguay. Thus, Bolivia presents a transition between the most representative ecosystems of the South American continent.

#### Data collection and conservation priorities determination

Data about the distribution and environment of *Serjania* species were gathered from the CTES Herbarium exsiccates and field trips, consist of 6 to 20 individuals per species and are listed in Supplementary material.

We used species richness as a measure of diversity and a criterion for establishing the conservation priorities for *Serjania*. We estimated this index in the 13 Bolivian forest formations by performing a 13 x 54 presence/absence matrix (Table 1), the species richness was estimated as following,

#### R=n*i*/N

Where: n/belongs to number of species in / cuadrant of the matrix and N is the total number of species analized.

In addition, to obtain an accurate spot for conservation, this analysis was performed in DIVA-GIS (Hijmans et al. 2005) using the Richness function and the number of different classes as output variable, a cell size of 1 x 1, and a simple point to grid procedure.

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

The effect of environmental conditions on the distribution of each species was estimated by fitting regression-tree models (hereafter, RT models; Breiman et al. 1984; De'ath and Fabricius 2000). This type of analysis considers spatiotemporal autocorrelation. For this analysis, the response variable was the number of specimens of each species per quadrat. To avoid deviation, we chose a quadrat size of 15m×15m, the smallest quadrat size that contained individuals. To check the robustness of results, we also included quadrat sizes of 50m×50m and 100m×100m in the analysis.

We obtained the 19 bioclimatic variables from the WorldClim database (Hijmans et al. 2013), which are listed in Table 2. These data are derived from monthly temperature and rainfall values with a spatial resolution of 2.5 arc-minutes (5 km<sup>2</sup>).

To detect collinearity and reduce redundancy among variables, we used a variance inflation factor (Dormann et al. 2007), which was estimated using Collinearity Diagnostic available in SPSS for linear regression analysis. We excluded variables with variance inflation factor greater than 3, following Zuur et al. (2010). A set of 10 climatic variables resulted non-redundant both in the present and in the future: 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).

Regression trees (RTs) predict a response to variables through binary decision trees based on combinations of predictor variables, similarly to the generalized linear models (GLMs). However, RT models are a better alternative than GLMs when multiple GLM assumptions are simultaneously violated. Moreover, RT models avoid overfitting the data. The cross-validation procedure used in this work takes into account spatial and temporal autocorrelation of the data.

An RT (Breiman et al., 1984) is a rule-based method that generates a binary tree. CART (Classification and Regression Tree algorithm) does not test a priori hypotheses about the relationships between variables. The algorithm splits a dataset (species occurrence) into several nodes based on yes/no answers to the predictor variables (environmental conditions). Thus, a binary tree is built. However, by predicting data in the growth of the tree a deviance is estimated; this is called resubstitution error and tends to overestimate the predictors even if these are pure noise. A typical tool to solve this problem is cross-validation, a resampling method that takes advantage of the entire dataset. Cross-validation consists of splitting the training

data set into n parts (usually 10). Each one of these sets is sequentially used as a test dataset in contrast to the tree model generated by the remaining N-1 subsets. Thus, we obtain different models that are used to assess the accuracy of regressions both in the training set (N-1) and in the test sets (N). Then the optimium tree can be selected when the accuracy is reached in either subset among all iterations. For our analysis, we used the "leave-one-out cross validation" (LOOCV) described by Arlot and Celisse (2010).

The RT was performed with the R package 'tree' (Ripley 2016), modified to add spatiotemporal LOOCV; RTs were subsequently converted to 'rpart' (Therneau et al. 2019) objects to evaluate the importance of each variable.

#### Present and future potential distribution of Serjania

To estimate the potential distribution of the species, we used ecological niche models (Peterson 2011, Anderson 2012). These models define the ecological niche through environmental layers associated with the species occurrence records, and identify areas with similar environmental conditions to those of the zones where the species would occur, discriminating areas with environments outside the species' ecological niche.

The potential distribution of the *Serjania* species and of the whole genus was generated using the Maxent software (Phillips et al. 2006). The procedure for generate the MaxEnt models used was the proposed by Mukherjee et al. (2011). In which the occurrences of *Serjania* were divided into 10 cross-validation partitions and every single partition consisted of 70% random points for model training and the remaining 30% points for extrinsic evaluation of models' predictive accuracy. The other MaxEnt parameters were left as default values. The accuracies of the Maxent prediction models were evaluated using both threshold-dependent and threshold independent approaches.

The predictions generated by Maxent were transformed into binary predictions in the threshold-dependent evaluation using the minimum training presence as the minimum predictive value in any location. In addition, was estimated the omission rate (OR) by corresponding test data points in the FPA (fraction of all predicted pixels) in accordance to Phillips et al. (2008).

The accuracy of the models was assessed using the area under the curve (AUC) of a receiver operating characteristic curve (ROC) measured as the average and standard deviation of the cross-validated replicate runs, using the ROCR package of R v. 3.1.2. This algorithm was chosen because it performs better than other environmental niche models (Elith et al. 2006, Hernandez et al. 2006, Aguirre-Gutiérrez et al. 2013). The models with the highest AUC and lowest average OR and FPA were selected for final MaxEnt model building. In accordance to Hosmer et al. (2000) we expected high accuracy and reasonable area of prediction in the selected models as optimum ones.

The 19 bioclimatic variables provided by Worldclim were used with a resolution of 30 seconds (Hijmans et al. 2005), which is sufficient to generate effective and efficient approximations of habitable environments *sensu* Bucklin et al (2015).

In addition, we estimated the future projection of the geographic distribution of the species of the genus under the rcp85 scenario for the 2050 year. This scenario assumes an increase of concentration of the greenhouse gases over the 21<sup>st</sup> century (IPCC 2014). Finally, to avoid discarding any occurrence record, the minimum training presence threshold was generated for both present and future in the final distribution.

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

### **Results**

# **Distribution patterns and Conservation priorities**

The highest *Serjania* species richness of all the Bolivian forest formations was recorded in the Chiquitano dry forest, followed by the Yungas (Fig. 2). Instead, the moist forest of the Precambrian shield and the wet savannas were the forest formations with fewest species of the genus (only one, in both cases is *Serjania glabrata*).

Of the 54 species analyzed, *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 restricted to the Chiquitano dry forest, whereas *S. circumvallata* Radlk., *S. communis* Cambess., *S. dumicola* Radlk., *S. leptocarpa* Radlk. and *S. mucronulata* Radlk. occurred only on the Yungas slopes. Two of the 54 species, *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. in the Inter-Andean dry valleys.

On the other hand, 7 species, *S. altissima* (Poepp.) Radlk., *S. caracasana* (Jacq.) Willd., *S. glabrata* Kunth, *S. hebecarpa* Benth., *S. longistipula* Radlk., *S. meridionalis* Cambess. and *S. sufferruginea* Radlk., presented a wide distribution, both in the country and in almost all Bolivian forest formations. The 28 remaining species were distributed in two to four forest formations.

According to the richness estimations made through DIVA-GIS, the richest regions belonged to the Yungas, in the department of La Paz, and to the Chiquitano dry forests in Santa Cruz department (Fig. 3). Thus, the conservation priorities should be established in the Yungas and Chiquitano dry forests, both considered tropical dry forests *sensu* Portillo-Quintero and Sánchez-Azofeifa (2010).

The best predictors for the presence of *Serjania* species were annual mean temperature, temperature annual range, annual precipitation, precipitation of driest month, and precipitation of coldest quarter (Fig. 4). Mean residual spatial autocorrelation was 187 m, with 500 m representing the case in which the variogram did not show signs of leveling-off, even at the maximum possible spatial lag of 500 m. Species belonging to the Chiquitano dry forest are characterized by occurring in a limited temperature annual range; this means that changes of more than 3°C (above or below) in the range of 19°C to 33°C did not allow the spread of most of the *Serjania* species growing in this type of environment. In turn, the species that occur in the Yungas were limited by annual precipitation, with this variable ranging between 2500 and 3500 mm.

### Present and future potential distribution of Serjania

The models resulted present a strong predictive power with AUC scores above 0.90, both in present as in the future also present low omission rate (OR) (0.002–0.005) values and FPA values ranged between 0.81–0.84.

The potential distribution of the *Serjania* genus in the American continent based on the data from Bolivia is illustrated in Fig. 5. In addition to the conservation hotspots established in Bolivia through the predictive results of our simulation, others can be located in the biogeographic regions of Caatinga, Cerrado and Chaco (Morrone 2006), i.e., the hotspots established through species richness and those located through predictive algorithms belong to the Amazon and Chaco subregions (Fig. 6). These results are consistent with the hypothesis that Bolivia would be a South American ecotone, as proposed by Ibisch (2005).

The future distribution of the genus and the increase or decrease of the occupied areas in the Americas in relation to the rcp85 scenario are illustrated in Fig. 7. Furthermore, the distribution of the following 12 species will be reduced: *S. ampelopsis, S. atrolineata, S. crassifolia, S. deltoidea, S. erecta, S. inflata, S. lethalis* (Fig. 8A, B), *S. longistipula, S. meridionalis* (Fig. 8C, D), *S. pyramidata, S. reticulata* and *S. sufferruginea*, and, *S. tenuifolia* will disappears completely from Brazil. On the other hand, *S. elongata, S. glabrata* (Fig. 9A, B), *S. mansiana, S. marginata* (Fig. 9C, D) and *S. sphaerococca* extend their distribution pattern. The most worrying case is *S. subrotundifolia*, which in 2050 would be extinct.

### Discussion

# **Distribution patterns and Conservation priorities**

Bolivia is a landlocked country of ca. 1 million square kilometers located in central South America and is considered one of the 17 megadiverse countries of the world (lbisch and Merida 2003). However, until the late 1980s, knowledge of the Bolivian flora was scarce (Solomon 1989). The situation has changed considerably in recent years and much progress has been made in documenting plant diversity in this country (Jørgensen et al. 2006). Current records indicate more than 12700 species of vascular plants (including ferns) and 1500 species of bryophytes.

Nevertheless, much work is still needed, and as in so many other tropical countries of the world, fragmentation and destruction of the natural habitat are the major threats to the long-term conservation of the Bolivian forests (Killeen et al. 2007). In this sense, the conservation of the secondary forest takes on great importance. This kind of forest is composed of woody vegetation that regrows after complete forest clearance for pasture, agriculture, or other human activities, such as clear-cutting for pulp (Faber-Langendoen 1992) or timber (Gorchov et al. 1993).

Secondary forest succession could be considered a continuum from an early stage, when factors that govern colonization gain more importance than in the later stages, when competitive ability and tolerance to environmental conditions among species largely drive patterns of species replacement over time (Walker and Chapin 1987). Both buried seeds and recently dispersed seeds contribute to the development of secondary vegetation. However, the proportion of soil-stored seeds available for forest regrowth appear to be more important (Garwood 1989), especially when land use intensity before abandonment was low to moderate (Ewel et al. 1981, Uhl et al. 1981). As intensity of land use increases, the potential of secondary forests to regenerate from soil-stored seeds diminishes. Therefore, the arrival of recently dispersed seeds plays an important role in forest regrowth, i.e., in the development of the secondary forest. At that point, the species of the genus *Serjania* play an important role, because their seeds are dispersed by wind.

In Bolivia, land is used for agriculture and timber extraction mainly in the areas adjacent to the Chiquitano dry forest (Steininger et al. 2001a, b, Pacheco and Mertens 2004), where records of mean deforestation rate have been 108,000 ha per year since 2001 (Killeen et al. 2006). This forest formation probably represents the largest extant patch of a Neotropical seasonal dry forest complex (Prado and Gibbs 1993, Prado 2000, Pennington et al. 2004), situated across a climatic transition between the humid evergreen forests of the Amazon and the deciduous thorn-scrub vegetation of the Gran Chaco. This forest had the highest *Serjania* species concentration.

Consequently, the conservation priorities of *Serjania* in the Chiquitano dry forest are due to the disturbance of the environment caused by land use and to the opportunistic character of this genus in altered environments, where it may initiate forest succession and regrowth. Moreover, several plant and animal species have the same conservation priorities in the Chiquitania (Killeen et al. 1998, Ibisch 2005, Linares-Palomino et al. 2011, Werneck et al. 2011) as those of *Serjania*, which reinforces the need for conservation of the Chiquitano dry forest or at least of some patches. In addition, the eight species that occur only in this forest are threatened in the country. Our results show that minimum changes in the temperature and precipitations ranges could lead to a severe reduction of the presence of these species. Finally, in the Americas, natural reserves protect almost 23,417 km<sup>2</sup> of tropical dry forest, which represents almost 5% of the total area covered by these biome (Olson et al. 2001). Of this 5%, two countries, Bolivia and Brazil, jointly are the main responsible for the protection of the tropical dry forest, with Bolivia being the country with largest protected area of tropical dry forest; of this area, almost 75% belongs to the Chiquitano dry forest, which is protected by a single park: the Noel Kempff Mercado National Park.

The second region in *Serjania* species richness, the Yungas slopes, coincides with the global conservation hotspot proposed by Myers (1988), Myers et al. (2000) and Brooks et al. (2006). The great concentration of plant and animal diversity (Killeen et al. 1998, Herzog and Kessler 2002, Swenson et al. 2012) and the low land use of the Bolivian Andean slopes encourage the conservation of this megadiverse region. Although Bolivia is a megadiverse country, there are not many endemic species; nevertheless, the diversity of each region is representative of almost all the types of environments of the South American subcontinent.

Both Chiquitano dry forest and the Yungas slopes belong to the Seasonally Dry Tropical Forest (SDTFs). This biome has a wide and fragmented distribution, from Mexico to Argentina and throughout the Caribbean, and is characterized by a closed canopy (Murphy and Lugo 1986, Gentry 1995). It occurs on fertile soils, where annual rainfall is below 1800 mm, with a period of three to six months receiving less than 100 mm per month, when the vegetation is mostly deciduous (Gentry 1995, Sánchez-Azofeifa 2005).

SDTFs are among the most threatened in the world because of intensive anthropogenic disturbance (Janzen 1988, Hoekstra et al. 2005); loss of this biome amounts to 72% in North and Central America, 66% in the Caribbean Island region and 60% in South America (Portillo-Quintero and Sánchez-Azofeifa 2010). Most of these losses are due to conversion to other land uses, such as agriculture, timber extraction, livestock production or urbanization (Hoekstra et al. 2005). Abandonment of these deforested areas was the main factor that led to regrowth as a secondary forest (Odum 1969).

The dynamics of the presence and distribution of *Serjania* in these South American SDTFs are strongly associated with narrow ranges of temperature and precipitation, except for the widely distributed species, which appear to present more plastic responses to environmental changes. The species that grow exclusively in the Chiquitano dry forest are highly influenced by temperature changes, which is expected in species occurring in this kind of environment (Allen et al. 2017; Pulla et al. 2021). Then, in these species, higher temperatures reduced the carbon assimilation rates (Vlam et al. 2013), which cause a direct negative impact on photosynthesis rates (Galbraith et al. 2010) and increasing autotrophic respiration rates (Clark 2010; Feeley et al. 2007), which means an increase in the cost of maintenance of plant tissues (Lloyd and Farquhar 1996).

Moreover, in tropical forests, an increment of air temperature of up to 10°C was found to lead to roughly a doubling of respiration rates (Meir et al. 2008). Temperature influences leaf-to-air vapor pressure deficit and evapotranspiration rates (Galbraith et al. 2010; Choat et al. 2012), and leaf stomata tend to close in order to reduce the water loss, resulting in lower CO<sub>2</sub> capture and reduced carbon assimilation rates (Lloyd and Farquhar 2008). Therefore, since in almost all the SDTFs the annual net primary production is concentrated in the rainy season, an increase of temperature during this time of the year could potentially cause losses or declines of species of *Serjania* strictly distributed in the Chiquitano.

On the other hand, the species with distribution restricted to the Yungas are susceptible to changes in the rainfall regime. These changes could alter the biodiversity and species ranges (Enquist 2002), reducing the secondary forest regrowth (Uriarte et al 2016). Reduced regrowth is very important, since *Serjania* species are promoters of secondary regrowth, which is fundamental for the restoration of altered ecosystems. Moreover, restoration of SDTFs after intense or prolonged droughts takes longer than that of moist tropical forest (Angeler and Allen 2016).

#### Present and future potential distribution of Serjania

The models performed well in predicting the current distribution of the studied *Serjania* species in the Americas (Macbride 1956, Ferrucci 1991, Jørgensen 1999, Robbins 2001, Acevedo-Rodríguez 2003, Ferrucci and Medina-Lemos 2013, Somner et al. 2015). Therefore, our results confirm the hypothesis that Bolivia is a South American ecotone and that it harbors of all the ecoregions of the continent.

Moreover, the potential distribution of the *Serjania* genus coincides with the current extent of the SDTFs (Portillo-Quintero and Sánchez-Azofeifa 2010, Banda et al. 2016), especially with those of central Brazil and Caatinga. This should not be surprising, because these environmental similarities are correlated with the affinities found by Banda et al. (2016) between the tropical dry forest of Bolivia and the other two forests.

The future projections for *Serjania* distribution suggest an increase of the SDTFs in southern areas of South America, which could be due to the increase in the maximum temperature expected by 2050 in accordance with the rcp85 scenario. These increments will lead to the connection of the Chiquitano dry forest with the Pantanal and the Cerrado of Brazil. In addition, an increase in the distribution of *Serjania* will cause the connection of the Mata Atlantica forest formation with the Caatinga region. These tropical dry forest expansions indicate a widespread reduction in precipitation across tropical South America, resembling the original distribution of the SDTFs (Prado and Gibbs 1993, Pennington et al. 2000, Prado 2000) in the Last Glacial Maximum (21,000 years before the present) *sensu* Werneck et al. (2011).

The mentioned increments of the Chiquitano dry forest and the surrounding SDTFs projected for the future are consistent with the proposal of Mayle et al. (2007): a progressive replacement of the rainforest by SDTFs and savanna of the Bolivia's Noel Kempff Mercado National Park over the 21st century in response to the increased drought and warming, which will cover almost all tropical South America. Moreover, Werneck et al. (2011)

predict that the SDTF nuclei (Caatinga and the Chiquitano regions) represent areas with long-term stability and very likely served as refuge areas during LGM. The species in these refuges are expected to have higher levels of genetic diversity than those in adjacent unstable areas; therefore, this forest formation can expand from the mentioned refuges.

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. SDTFs are the most extensive and important tropical vegetation types in these regions (Murphy et al. 1995), and are distributed along the Pacific Coast from the Tropic of Cancer to northern Costa Rica (Pennington et al. 2000). 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 (Maass et al. 1995). 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 (Trejo and Dirzo 2000).

These increments and decreases in the distribution area of the genus, and the connection of ecosystems could be due to the conversion of the original forest to agriculture or timber exploitation, the subsequent abandonment and secondary forest regrowth, as also was predicted by Rodrigues et al. (2015) in trees of the Brazilian SDTFS

Tropical secondary forests are important timber sources (Wadsworth 1997) and providers of environmental services such as protection from erosion and atmospheric carbon fixation (Fearnsides and Guimaraes 1996). However, the regenerative potential of SDTFs is high only if propagule sources are available and land use intensity before abandonment has not been severe (Guariguata and Ostertag 2001). Moreover, in environments with severe abiotic stress, pioneer woody species often act as nurse plants, ameliorating microclimatic conditions and enhancing soil nutrients (Flores and Jurado 2003).

In open areas, nurse plants provide 'fertility islands', where more favorable conditions for establishment are found (Pugnaire et al. 1996). Thus, facilitation by nurse plants plays an important role in maintaining the diversity of harsh environments by increasing species richness at the community level (Hacker and Gaines 1997, Cavieres and Badano 2009, Cavieres et al. 2014). However, since different pioneer species can have contrasting effects beneath their canopies, species-specific patterns are likely to emerge. Several mechanisms may generate species-specific plant interactions and are linked to different ways in which nurse plants influence resources and conditions, such as soil water content, nutrient availability, microclimate and herbivore pressure (Callaway 1998). The outcome of plant–plant interactions between nurse and beneficiary species will also depend on the ecological strategy of the beneficiary species and how they rely on the resources provided by nurses (Liancourt et al. 2005, Maestre et al. 2009).

We consider the species of the *Serjania* genus as nurse species because they facilitate the establishment of plants that contribute to forest regrowth; by providing nutrients and shade (Padilla and Pugnaire 2006) and occur in a wide range of environments associated with anthropized areas, an important role in post-disturbance habitat restoration.

This role of *Serjania* is not an outlandish idea, since Schnitzer et al. (2000) identified three pathways in gap-phase regeneration: palms, small trees and lianas. Moreover, DeWalt et al. (2000), Kuzee and Bongers (2005) and Madeira et al. (2009) highlight the highest liana species richness in early to intermediate stages of succession, which makes *Serjania* a good candidate for facilitating the establishment of new vegetation growing during secondary succession. Putz (1984) and Schnitzer et al. (2000) indicate that the proportion of pioneer trees in gaps is positively related to the abundance of lianas. Then, the subsequent increase of shade generated by lianas promotes the decrease of their abundance. In *Serjania* this mechanism could be more marked, because species with tendril climbing strategies decline over time as the availability of small-diameter supports diminishes (Putz and Holbrook 1991, DeWalt et al. 2000), i.e., as the forest becomes older, as proposed by Schnitzer and Bongers (2002).

Therefore, *Serjania* could play a crucial role in the post-disturbance recovery of the forest in the long term, i.e., more than 40 years (DeWalt et al. 2000). Hence, the preservation of high lianas richness spots acquires importance to guarantee the full restoration of the forests.

### Conclusion

Bolivia and Brazil harbor the largest fragments of the seasonally dry tropical forest in the world (Portillo-Quintero and Sánchez-Azofeifa 2010). In addition, the seasonally dry tropical forest is one of the most threatened tropical terrestrial ecosystems because these zones were historically preferred for agriculture and human settlement in the Americas (Sánchez-Azofeifa et al. 2005, Pennington 2006, Ewel 1999). However, few studies have been conducted on the natural regeneration necessary to restore these forests. We found that *Serjania* is an important representative of this kind of forests, especially in the Chiquitano dry forest and Yungas slopes, where we established the conservation priorities for the genus. The location of the conservation spots of these forests is not surprising, since Yungas is already one of the global hotspots of conservation established by Mayle et al. (2007) and the Chiquitano dry forest is one of the most stable forests along with Caatinga, both of which acted as refuge for the dry flora during the LGM. In addition, our study agrees with several others that also establish the conservation priorities in the Chiquitano dry forest due to its high biodiversity.

Moreover, the key role of lianas, such *Serjania* spp. in the secondary succession of the forest, confirmed in this work, makes this genus important because its conservation would ensure forest restoration after disturbance.

Finally, the projection of the future distribution of the genus supports the prediction in the distribution of the SDTFs from the Chiquitano dry forest and the Caatinga provided by Werneck et al. (2011). Therefore, the integral conservation of the spots established in this work guarantees the integrity of the tropical dry forest and the successful restoration of the altered landscape previously occupied by these ecosystems.

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### Tables

 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	0001	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
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
Species/Forest Formation	AF	Yu	ChF	CDF	MMF	CF	TBF	MS	MPF	PS	IDV	CMF	AmF
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

**Table 2.** Average bioclimatic variables for all species studied, BIO 1 = annual mean temperature, BIO 2 = Mean monthly temperaturerange, BIO 3 = Isothermality, BIO 4 = Temperature seasonality, BIO 5 = Max temperature of warmest month, BIO 6 = Mintemperature of coldest month, BIO 7 = Temperature annual range, BIO 8 = Mean temperature of wettest quarter, BIO 9 = Meantemperature of driest quarter, BIO 10 = Mean temperature of warmest quarter, BIO 11 = Mean temperature of coldest quarter, BIO 12 = Annual precipitation, BIO 13 = Precipitation of wettest month, BIO 14 = Precipitation of driest month, BIO 15 = Precipitation

seasonality, BIO 16 = Precipitation of wettest quarter, BIO 17 = Precipitation of driest quarter, BIO 18 = Precipitation of warmest quarter, BIO 19 = Precipitation of coldest quarter.

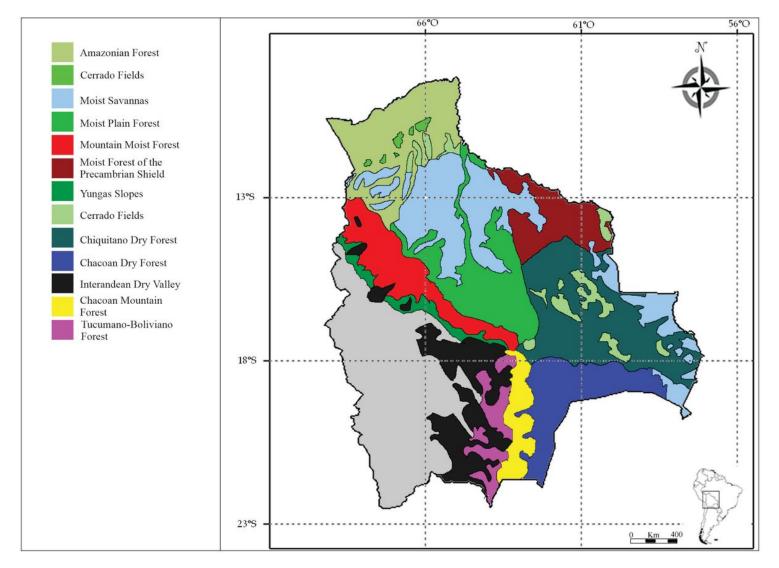
Species	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
S. altissima												1304.57				593.17	94.70		113.26
S. ampelopsis	25.12	13.16	66.27	22.70	28.13	7.98	20.14	28.04	16.87	28.62	16.09	870.75	153.17	11.67	65.51	427.92	56.50	389.42	70.75
S. atrolineata	22.33	11.25	65.34	21.67	30.06	12.84	17.22	24.40	19.69	24.40	19.33	1066.20	186.80	24.60	64.39	495.60	99.40	494.60	114.80
S. caracasana	23.50	12.98	64.61	25.80	32.61	12.41	20.20	25.53	21.47	25.73	20.33	1046.70	178.91	16.35	68.93	494.09	70.52	380.57	98.96
S. meridionalis	23.84	12.84	65.13	22.76	31.17	11.17	20.00	24.12	19.48	26.68	19.02	1139.42	195.13	19.83	66.56	538.71	79.71	422.38	70.15
S. chaetocarpa	24.25	13.55	69.16	15.80	33.04	13.44	19.60	25.36	22.19	25.58	21.97	1334.14	233.00	17.29	69.67	632.57	70.29	347.71	104.43
S.																			
circumvallata												1792.00				777.00		705.00	-
S. comata		12.71										1105.67				497.00	98.33		118.00
S. communis S. confertiflora			74.97									1027.00				519.50	61.50	430.00	-
												1164.00 1411.58				528.73	93.00		119.38
S. crassifolia S. crassifolia												1411.58				643.00 643.00		516.89 516.89	-
S. deltoidea												1568.33				696.56	136.89		146.56
S. dibotrya												1421.00				652.33	91.67		117.00
S.dydymadenia												1735.75				764.50			-
S. diffusa			70.00										140.00	8.40	84.69	386.60	32.20	323.60	37.00
S.dumicola			72.48				18.88					992.40	202.00			528.40	47.80	398.80	58.40
S. elongata	25.14	12.04	69.16	13.99	33.17	15.77	17.40	26.13	23.53	26.31	23.10	1626.33	259.67	37.67	60.52	716.00	136.67	407.67	166.00
S. erecta	23.32	13.87	68.90	24.02	32.43	12.27	20.16	24.51	21.18	24.76	20.95	1279.50	218.92	18.08	67.00	599.67	76.50	328.67	107.42
S. foveata	17.49	13.39	65.94	23.99	26.54	5.96	20.58	19.96	14.77	20.01	14.20	678.57	136.21	6.57	82.59	379.36	24.00	354.29	27.29
S. fuscifolia	24.02	12.95	67.12	21.95	33.00	13.70	19.30	25.96	21.62	26.09	20.98	1087.00	169.67	19.00	56.56	464.67	96.33	403.67	131.67
S. glabrata	21.56	17.13	63.31	26.40	29.16	7.81	21.35	22.30	16.75	22.52	17.38	839.80	161.02	10.11	68.64	446.51	38.91	384.27	48.27
S. grandiceps	25.72	10.83	69.00	10.39	33.10	17.40	15.70	26.30	24.40	26.63	24.12	1746.00	268.00	34.00	59.39	749.00	120.00	435.00	150.00
S. hebecarpa												1084.24				501.62	85.21		117.21
S. inflata	22.97	11.09										1438.00				636.86		516.00	-
S. leptocarpa		10.98										1547.00				692.67		622.33	-
S. lethalis												1179.58				547.42	84.42		106.68
S. leucosepala												1453.00				684.00	110.00		150.00
S. longistipula			69.25			5.06					19.57		157.43		78.44	427.71	37.00		-
S. mansiana S. marginata												1273.19 1095.88				588.50 491.88	104.00 88.56		112.40 117.72
S. meridionalis												1139.42				538.71	79.71	422.38	-
S. minutiflora												1053.83				451.92			-
S. mucronulata			73.20									1112.50				550.50	61.50	368.50	-
S. neei		11.82			29.10								139.00			388.00	93.00		118.00
S. noxia												1494.75				694.75	62.25		101.00
S. nutans												1557.83				692.17	132.50	599.67	140.33
S. orbicularis	23.22	14.11	68.39	18.64	32.60	11.95	20.65	24.61	20.69	24.84	20.59	1158.17	194.17	19.83	64.49	540.00	83.17	334.67	109.50
S. ovalifolia	23.93	13.51	70.36	13.09	32.50	13.30	19.20	24.80	22.20	25.05	22.00	1455.00	258.00	14.00	71.78	689.00	64.00	330.00	99.00
S. paludosa	24.49	12.42	66.24	19.45	32.70	14.00	18.70	26.08	22.33	26.15	21.71	2321.00	371.00	65.00	58.32	1005.50	228.00	856.00	99.00
S. pannifolia	22.80	19.86	70.42	25.46	30.41	13.83	16.58	23.73	21.09	23.92	21.01	1429.00	234.55	21.91	64.85	653.00	92.82	471.64	111.82
<i>S.</i>	00.07	10		40.05	00.00	40.11	10.00	04.05	00 0 <del>.</del>	0- 0-	00.11		0.5.5.0.5			005.00		000.05	00.00
paucidentata												1451.00				687.00	64.00	329.00	-
S. perulacea												1088.47				510.87	79.33		107.40
S. platycarpa												1157.15				522.69 674.40		427.00	-
S. pyramidata S. reticulata												1498.60 1315.19				674.40	93.48	514.80 433.52	146.00
S. rubicaulis												1315.19				605.24		433.52	-
S. rubicunda												1278.00				596.00	75.00		109.00
S. setigera												1060.00				460.00		444.00	-
S. souzana												2038.50				860.50		741.00	-
S. sphaerococca												1271.25					106.06	488.69	129.19
S. subrotundifolia	24.11	11.99	66.73	17.90	32.05	14.15	17.90	25.65	21.68	25.75	21.57	1515.50	279.00	27.00	66.92	719.00	113.00	540.50	131.00
S. sufferruginea	18.62	13 30	66 39	23.27	27 66	7 10	20.47	20.05	24 52	21.04	23 80	814 60	163.00	9.20	66.96	443.90	36 60	385.50	42 00
S. tenuifolia												814.60 1641.63						507.75	-
S. tripleuria												911.43				466.43		429.48	-
5. u ipieulia	44.00	13.20	50.23	54.74	52.00	5.07	23.01	20.49	13.00	40.90	10.1/	JII.43	100.33	0.32	00.07	400.43	50.52	449.40	00.30

## Declarations

Author Contributions: JPC and MCB conceived and designed the experiments. JPC performed the experiments and analyzed the data. JPC and MCB wrote the manuscript.

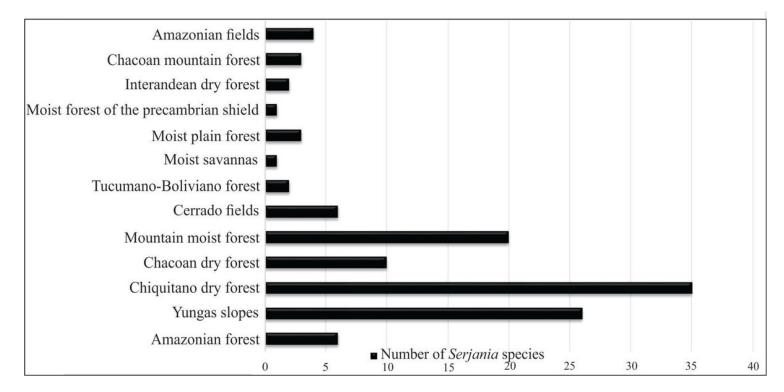
Data availability: The authors declare that all data supporting the findings of this study are available within the article and its supplementary information files.

## Figures

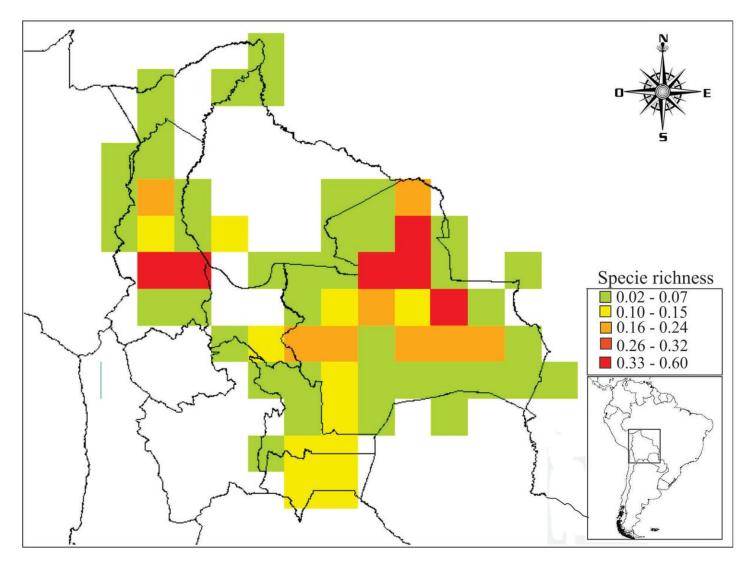


### Figure 1

Bolivian forest formations in accordance to Killeen et al. (1993)



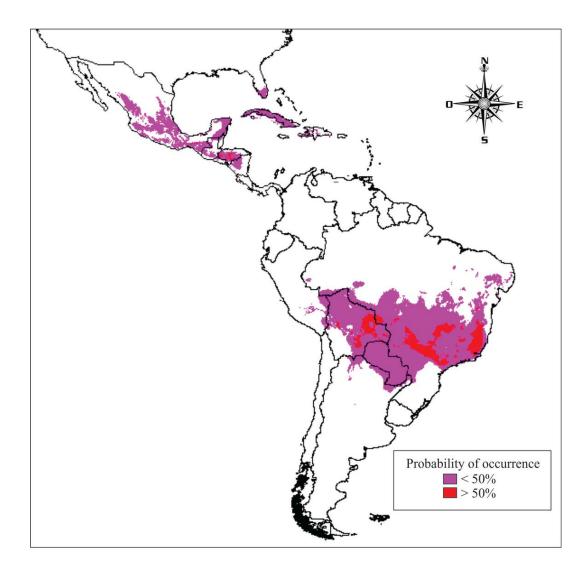
Number of *Serjania* species regarding to each Bolivian forest formation *sensu* Killeen et al. (1993) in which is remarkable the high number of it in the Chiquitano dry forest followed by the Yungas slopes.



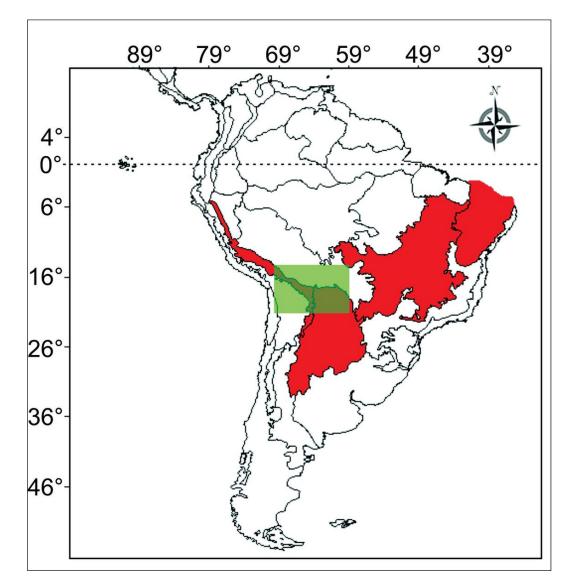
Species richness estimation of *Serjania*, the richest spots are located in La Paz and Santa Cruz departments in which would be established the conservation priorities. These spots coincide with the Yungas slopes and Chiquitano dry forest.

	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	Importance
S. dibotrya	4	1	1	10	0	15	2	28	0	1	-
S. didymadenia	38	1	1	13	0	16	1	23	1	0	60
S. diffusa	0	0	0	21	2	14	1	15	0	14	
S. dumicola	0	0	0	6	8	22	0	19	2	23	10
S. elongata	14	0	1	12	0	30	0	3	2	24	40
S. erecta	23	0	0	0	1	0	2	5	1	9	
S. foveata	5	1	2	8	6	33	2	16	0	18	20
S. fuscifolia	35	0	8	27	4	2	3	10	5	3	20
S. glabrata	1	4	0	0	1	15	0	13	0	20	
S. grandiceps	25	3	1	24	0	7	1	8	2	22	0
S. hebecarpa	3	4	6	9	0	4	1	1	2	11	0
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	

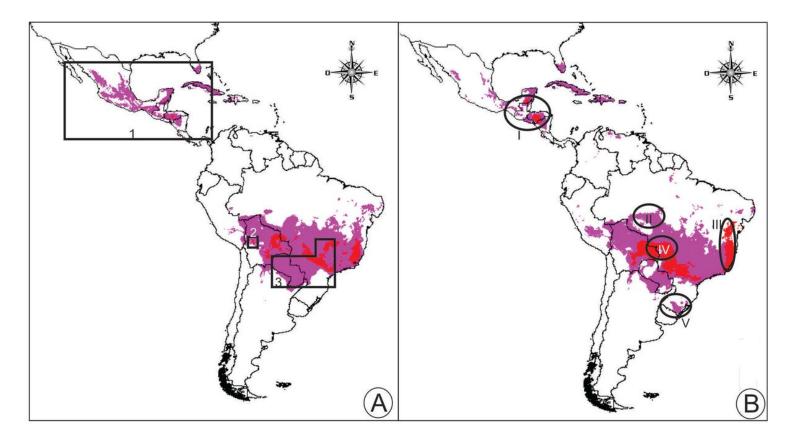
Variable importance for the presence of Serjania species. The variable importance scores signify of the fit resulting from the selection of a determined variable and the number of times that appear either as primary variable or as a surrogate one. Higher numbers explain mor of the variance of a predictor. 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.



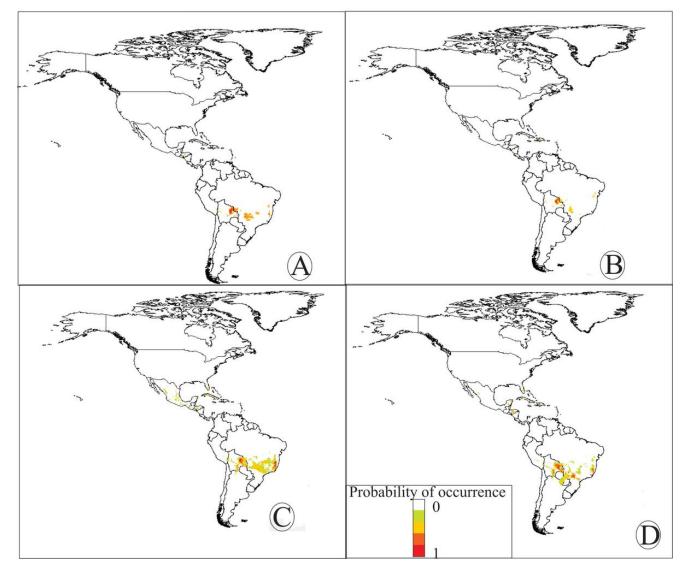
Projection of the present genus distribution in America based in the occurrence of Serjania in Bolivia.



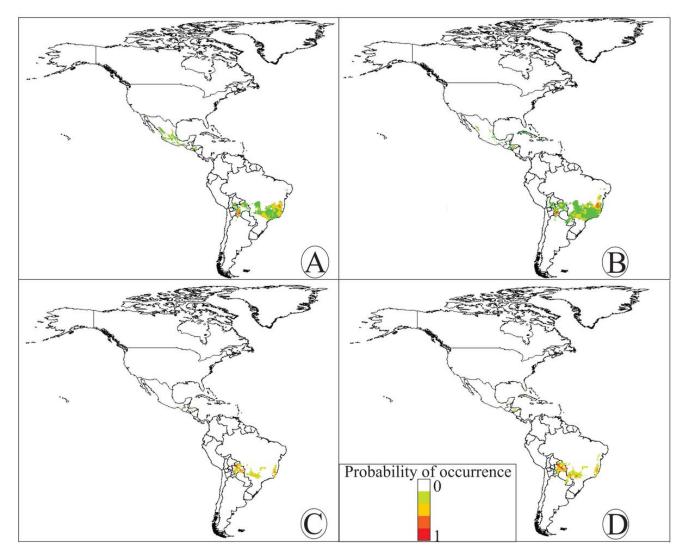
Conservation hotspots situated in the biogeographical provinces proposed by Morrone (2006), in Bolivia Yungas and Chaco provinces, the yellow rectangle shows where must be placed the conservation hotspot, and in Brazil Caatinga and Cerrado ones.



Present (A) and Future (B) distribution of *Serjania* in America regarding to the rcp 85 scenario. 1, 2, 3 in (A) represent losses in the land covering of the *Serjania* based in the genus occurrence in Bolivia in relation with the future scenario choosing and, I, II, III, IV, V represent increase of the concentration of the species and land covering of *Serjania* based on the same than previous.



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



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

# **Supplementary Files**

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• Supplementarymaterial.docx