



Leguminosae endemic to the Chaco facing quaternary climate fluctuations

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ABSTRACT

We investigated the influence of Quaternary climate fluctuations on the current distribution of three species of Leguminosae (Fabaceae) occurring in the Chaco. Potential distribution models of *Bauhinia hagenbeckii*, *Muelleria nudiflora* and *Neltuma rubriflora* with a supposed endemism area were generated. The Last Interglacial, Last Glacial Maximum, Holocene Middle and current scenarios were used. The species showed a potential distribution according to the South American biogeographic history regarding the glacier regression and the formation of the Dry Diagonal. The models for each Quaternary event exhibited a tolerable AUC ≥ 0.9 for the validations. The LGM was the event that favoured the current species establishment areas in the Dry Diagonal. Quaternary climatic events were related to the current Leguminosae distribution. *Bauhinia hagenbeckii* and *Neltuma rubriflora* present similar areas of environmental suitability. *Muelleria nudiflora* models with areas of environmental suitability were larger for the LIG and Holocene than for areas from other periods. All scenario models (LGM, HM and current scenario) highlighted the potential distribution of the three species concomitant with the glacier regression events and were consistent with the history of formation of South American dry areas.

Keywords: biogeography, dry areas, Fabaceae, species distribution, ecological niche modelling

Introduction

On a global scale, Leguminosae serve as a model for studies based on phytogeographic approaches since they are a highly successful group occupying most of the terrestrial habitats such as dry, humid and temperate rainforests, savannas, fields, and deserts, thereby representing the

protagonists of the global (Schrire *et al.* 2005) and regional biota, mainly in the Neotropics (Simon & Proença 2000; Flores & Miotto 2005; Flores & Tozzi 2008; Cardoso & Queiroz 2011; Werneck 2011; Morales *et al.* 2019). The Chaco, the largest continuous area of dry forests in South America, has a high richness and endemism when compared to other dry areas (Dryflor 2016). This aspect is favoured by the climatic seasonality of the domain, with hotter summers

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reaching high temperatures, which may explain the greater richness of Leguminosae species, since the family is highly adapted to hot and dry environments (Lima *et al.* 2015; Bueno *et al.* 2017; Hoyos *et al.* 2018).

A number of floristic studies have shown the Leguminosae richness in the Chaco (Adámoli *et al.* 1972; Ortega-Torres *et al.* 1989; Lewis 1991; Spichiger *et al.* 1991; Navarro *et al.* 2006; Noguchi *et al.* 2009; Torrela *et al.* 2011; Gimenez *et al.* 2011; Giorgis *et al.* 2011; Freitas *et al.* 2013; Neves *et al.* 2015; Souza-Lima *et al.* 2017; Sartori *et al.* 2018; Morales *et al.* 2019; Sinani *et al.* 2019). In addition, species such as *Bauhinia hagenbeckii*, *Muelleria nudiflora* and *Neltuma rubriflora*, of restricted distribution, suggest areas of endemism in the Chaco wet sector (Wunderlin 1968; Burkart 1969; 1976; Vaz *et al.* 2010).

Data about the high Leguminosae diversity in the Chaco (Lima *et al.* 2015; Morales *et al.* 2019), together with the geographic distribution records of the group have been reported in several studies (Morales *et al.* 2019), provide support for the biogeographic hypotheses of the Chaco formation, important for the understanding of historical relationships and the evolution of the Dry Diagonal flora (Prado 2000; Cardoso & Queiroz 2011; Mogni *et al.* 2015; Neves *et al.* 2015).

The evolution and distribution of the South American species occurring in dry areas was shaped by the Quaternary climatic fluctuations, with expected events of population expansion following the expansion of suitable habitats and population extinctions in response to the retraction of habitat suitability, as well as populations restricted to refuges (Haffer 1969; Haffer & Prance 2001; Graham *et al.* 2006; Bueno *et al.* 2017; Rezende *et al.* 2018). The Last Interglacial (between 120,000 and 140,000 years before the present) was characterized by warmer temperatures, greater summer insolation, prominent thawing, sea level rise, and forest expansion (Otto-Bliesner *et al.* 2006). In the Last Glacial Maximum (*ca.* 22,000 years before the present), the climate became drier and cooler, with a decrease of some area of the Amazon rainforest replaced by native fields leading to an intense landscape change (Behling 2002). The end of this scenario was marked by the glacier retreat approximately 8,000 years ago and the return of the rains. In contrast, in the Middle Holocene (*ca.* 6,000 years before the present) the climate became warmer and entered a phase called the climatic optimum, when the earth was about 2 to 3° C warmer and had greater precipitation than currently (Souza *et al.* 2005).

The Chaco was probably formed more recently than the other Dry Diagonal areas, with the current composition of Chaco biota being influenced by external sources to a greater extent. The areas of the Seasonally Dry Tropical Forests (SDTF) and the Chaco were considered distinct and there is an intercalation between the biomes of South America, especially the dry diagonal in Brazil (Silva de Miranda *et al.* 2018). In addition, it is possible that low

elevation Chaco regions were more affected by Quaternary climatic fluctuations than other open ecoregions located at higher elevations, so that interglacial rises in sea level may have been sufficient to inundate many Chaco areas (Werneck 2011). The Pleistocene climate was arid during the dry periods, with extended scrub vegetation and even steppe through at least the western Chaco. During more wet periods the vegetation was lush than currently in the western Chaco, particularly along water courses. Large swamps and extensive palm savannas fringed with forest probably characterized the eastern Chaco during wet periods. Embayment of the lower Parana River during interglacial periods may have occurred in conjunction with high ground water and extensive swamps from Central-Western Brazil to the delta of the Paraná. Full glacial periods were probably characterized by very dry conditions, at least in the western Chaco (Short 1975). This suggests that the Chaco has undergone the greatest boundary shifts, and its ecologically generalist fauna could easily find refuge in open vegetation formations at higher elevation (*e.g.* surrounding Cerrado and SDTF remnants). As a result, these supposedly less stable Chaco areas across climatic fluctuations have been considered to shelter a less differentiated fauna, with lower levels of intraspecific genetic diversity when compared to populations from the other two open dry areas. Phylogenetic studies of a Leguminosae group (*Caesalpinia*) carried out in the pantropical region and in the Chaco have shown phylogenetic conservatism in the biome (Gagnon *et al.* 2019). However, the Chaco's central location is strategically placed in a very active ecotonal region, where many different vegetation types meet, possibly representing a region of 'current evolutionary history' crucial to the dynamics of many species. Ecotonal areas are potentially important regions of differentiation and speciation, thus having a great evolutionary potential (Werneck 2011).

Consequently, paleodistribution modelling provides a method for the production of spatially explicit models of landscape dynamics over recent time scales (*e.g.* Quaternary) (Pennington *et al.* 2000; Werneck *et al.* 2011; Bueno *et al.* 2017). The Ecological Niche Modelling (ENM) has become a popular tool in phylogeography, evolutionary biology and conservation biology for the inference of potential geographic distributions of species in past, present and future climatic conditions (Chan *et al.* 2011). In this regard, modelling can produce models of potential distribution in biogeographic analyses conducted for different purposes. Thus, the use of models generated by modelling can support actions for the conservation of rare or endangered species, reintroduction of species, detection of biodiversity loss, assessment of the impacts of climate change, invasive potential of exotic species, and conservation priorities (Giannini *et al.* 2012). In this context, the aim of this study was to determine the effects of the Quaternary climatic fluctuation on the current distribution of three endemic Leguminosae species occurring in the Chaco based on the



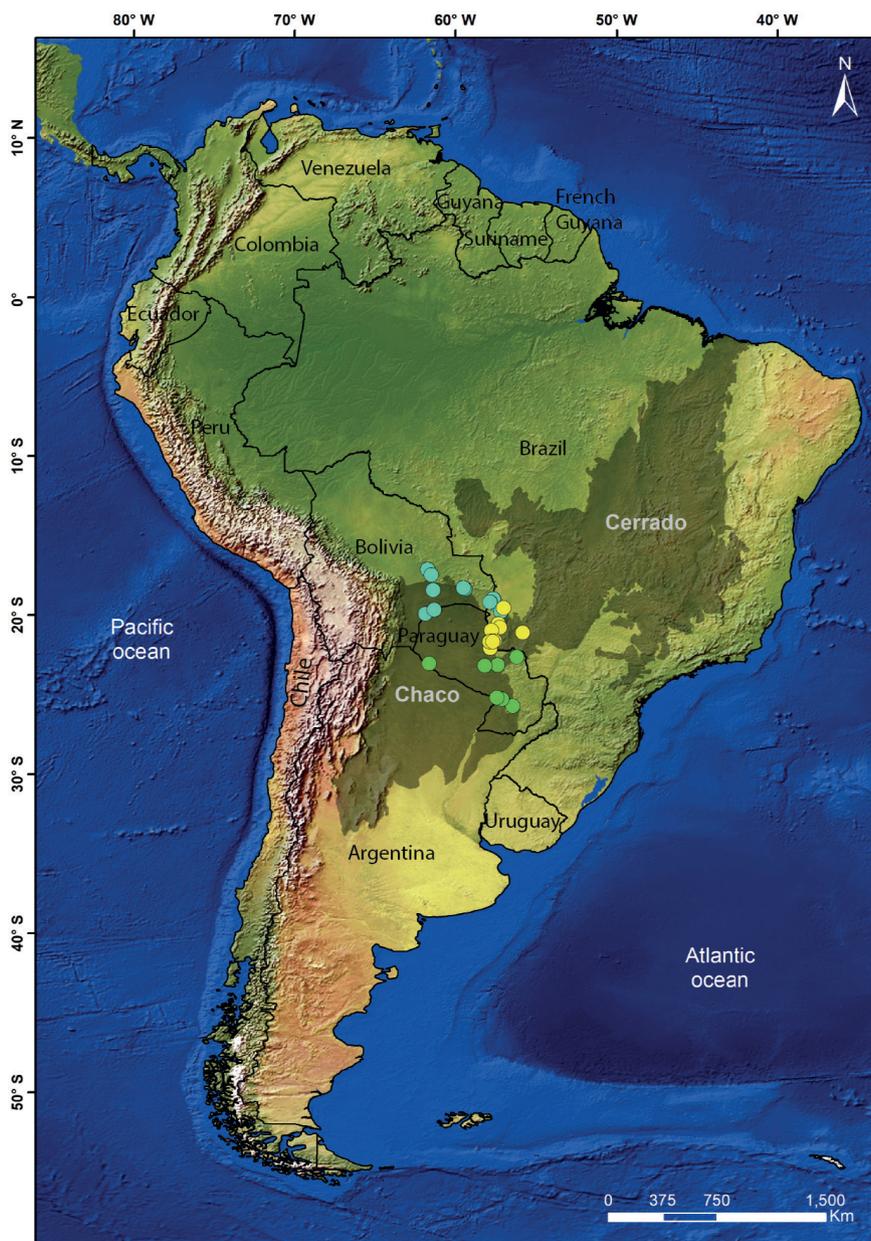
following questions: i) whether there was an expansion or contraction of the occurrence of Leguminosae species in the Chaco during the Last Glacial Maximum (LGM) and/or Last Interglacial (LIG); ii) whether the LGM was the event that favoured the current species establishment areas in the Dry Diagonal, as also highlighted in previous studies.

Materials and methods

Study site

The study covered the Chaco region including the areas of occurrence of the studied species (Fig. 1). The Chaco

occurs in the south-central region of South America, with an area of more than 800,000 km² extending from the northern and central regions of Argentina, eastern Paraguay and south-east Bolivia to the extreme west of the Mato Grosso do Sul state, Brazil (Hueck 1972; Prado & Gibbs 1993). This domain is located in a lowland characterized to a sedimentary basin of thin, wind-blown soils (loess) deep and compacted, almost without rocks, which impair water infiltration, usually leaving the water table out of reach of the roots of the plants (Zanella 2011). The climate has a strong seasonality, with maximum summer temperatures as high as 49° C, the highest temperatures recorded in South America, and severe winter frosts (Pennington *et al.* 2000). Rainfall ranges from over 1000 mm/year to the east to less



Bauhinia hagenbeckii



Muellera nudiflora



Neltuma rubriflora

Figure 1. Map of South America with the Chaco and Cerrado delimitation and places of occurrence of *Bauhinia hagenbeckii* (green), *Muellera nudiflora* (blue) and *Neltuma rubriflora* (yellow).

than 500 mm/year to the west, with a dry season in winter and spring and a rainy season in the summer. The dry season has a longer duration from east to west (Pennington *et al.* 2000). Vegetational formations or open arboreal vegetation commonly grow in the Chaco, the latter characterized by spinous, deciduous species with small leaves and xerophytic characteristics (Hueck 1972).

Species data and delimitation

Data from CGMS (Brazil), FCQ (Paraguay) and PY (Paraguay) herbaria and digitized herbarium data were used to obtain the geographic location of the species studied (biotic data) and later species distribution modelling available at GBIF (Global Biodiversity Information Facility, <http://www.gbif.org/>) and SpeciesLink (<http://inct.splink.org.br/>) (Tab. S1).

In this study, we selected species with areas of endemism in the Chaco region such as *Bauhinia hagenbeckii* Harms, *Muelleria nudiflora* (Burkart) M.J. Silva & A.M.G. Azevedo and *Neltuma rubriflora* (Hassl.) C. E. Hughes & G. P. Lewis. *Bauhinia hagenbeckii* occurs in the wet areas of the Chaco in Paraguay and Brazil (Wunderlin 1968). *Muelleria nudiflora* is found mainly in the areas of Bolivia, Paraguay and Brazil (Burkart 1969) (Fig. 1). In Brazil there are records only for the Mato Grosso do Sul state (Silva & Tozzi 2015). *Neltuma rubriflora* is an important indicator of Chaco wet areas and occurs in Paraguay (Burkart & Simpson 1977) and Brazil (Souza-Lima *et al.* 2017).

Data analyses

Environmental predictors consisted of bioclimatic variables interpolated from climate data between 1950 and 2000 obtained from the Worldclim dataset (Hijmans *et al.* 2005; <http://www.worldclim.org>). The 19 standard variables at 2.5 arc-min (approximately 5 km) resolution reflect various aspects of temperature, precipitation, and seasonality, which are likely to be important in determining species distributions. The bioclimatic layers were cropped covering all South America. We used a stepwise procedure implemented in the R sdm package (Naimi & Araújo 2016) in R 3.6.3 (R Development Core Team 2021) to test the issue of multicollinearity among the environmental variables by estimating the variance inflation factor (VIF) and retained only the variables with VIF < 10 (Graham 2003). This reduced our number of environmental predictors to eight.

To verify the palaeodistribution of *Bauhinia hagenbeckii*, *Muelleria nudiflora* and *Neltuma rubriflora* in the late Quaternary climatic changes, we produced suitability projections of occurrence during the Current (0 ka pre-industrial), Mid-Holocene (6 000 BP), Last Glacial Maximum (LGM – 22 BP), and Last Interglacial (LIG ~ 130 BP) time periods, based on climatic simulations (Hijmans *et al.* 2005). For the Last Glacial Maximum (21 LGM) and Holocene (6 BP time periods) we employed the Community Climate System Model - CCSM4 (Gent *et al.* 2011) and MIROC-ESM

(Watanabe *et al.* 2011) which represents downscaled climate data from simulations with Global Climate Models (GCMs) based on the Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor *et al.* 2012). We summed the projections of the species for each time period, which together represent the probability of occurrence during that time period. The paleo-climatic model for the Last Interglacial (120 ka, LIG) data were obtained from Otto-Bliesner *et al.* (2006).

We fitted ENMs for each species using four modelling algorithms implemented in the sdm package in R (Naimi & Araújo 2016). These were maximum entropy (MaxEnt) (Phillips *et al.* 2006); random forests (rf) (Breiman 2001); generalised linear models (glm) (McCullagh & Nelder 1989), and BIOCLIM (bioclim.dismo) (Hijmans & Graham 2006). These methods were used to link the current environmental conditions to the species presence and absence data, and subsequently to predict and map the spatial distribution of the species for the current and paleoclimatic projections. All models were calibrated with presence only data combined with 1,000 randomly selected pseudo-absence records for each species across the study area, generated with the R sdm package (Naimi & Araújo 2016). We built ensemble models combining multiple replicates of several different modelling algorithms (Araújo & New 2007). Due to their combined power, ensemble models are widely accepted to provide more accurate results than single models (Forester *et al.* 2013).

To assess the predictive capacity of the models, we divided the data for each species into a training set (70 % of occurrence) and a test or validation set (30 % of occurrence) performed with the ten replicate subsampling method. We measured the accuracy of the models using the area under the Receiver Operating Characteristic (ROC) curve (AUC) and the True Skill Statistics (TSS) value (Bradley 1997). Models with values above 0.75 are considered to be potentially useful (Elith *et al.* 2011). Several statistical indicators can be used as metrics to evaluate model performance (Fielding & Bell 1997). To validate the produced models, we used the Area Under Curve (AUC) as a threshold-independent measure and the True Skill Statistic (TSS) as threshold-dependent accuracy measures (Allouche *et al.* 2006; Liu *et al.* 2009) and produced the binary maps.

Results

The model performance for three species was better than random, with a mean training AUC value ranging from 0.94 to 0.99 and a TSS value ranging from 0.89 to 0.99, indicating that the model performed well in predicting the suitable habitat area for the species. The relative contributions of the most important environmental variables determining the distribution of *Bauhinia hagenbeckii*, *Muelleria nudiflora* and *Neltuma rubriflora* according to the models were: Bio10 (Mean Temperature of Warmest Quarter) (74 %) and Bio19 (Precipitation of Coldest Quarter) (26 %), Bio3



(Isothermality), Bio15 (Precipitation Seasonality) with 25%, and Bio18 (Precipitation of Warmest Quarter) with 8%. These were the most important environmental variables determining the distribution of *Bauhinia hagenbeckii*, *Muelleria nudiflora* and *Neltuma rubriflora*.

The models of *B. hagenbeckii* (Figs. 1, 2, 3) showed the smallest areas of environmental adequacy at present compared to the other periods. The present models suggest areas of possible environmental suitability with a continuous area of occurrence for the species located in the area of

current occurrence records. The LIG models suggest areas of disjointed environmental suitability of Colombia, Venezuela, Guiana and Suriname, occupying areas of the Forests and regions of Bolivia and Argentina. The models also suggest southern occupation of Chile throughout the past. The variations of the LIG, LGM and Holocene models suggest the favouring of endemism since there was a suggestion of a decrease in the areas from the past to the present time.

Muelleria nudiflora models with areas of environmental suitability were larger for the LIG and Holocene than for

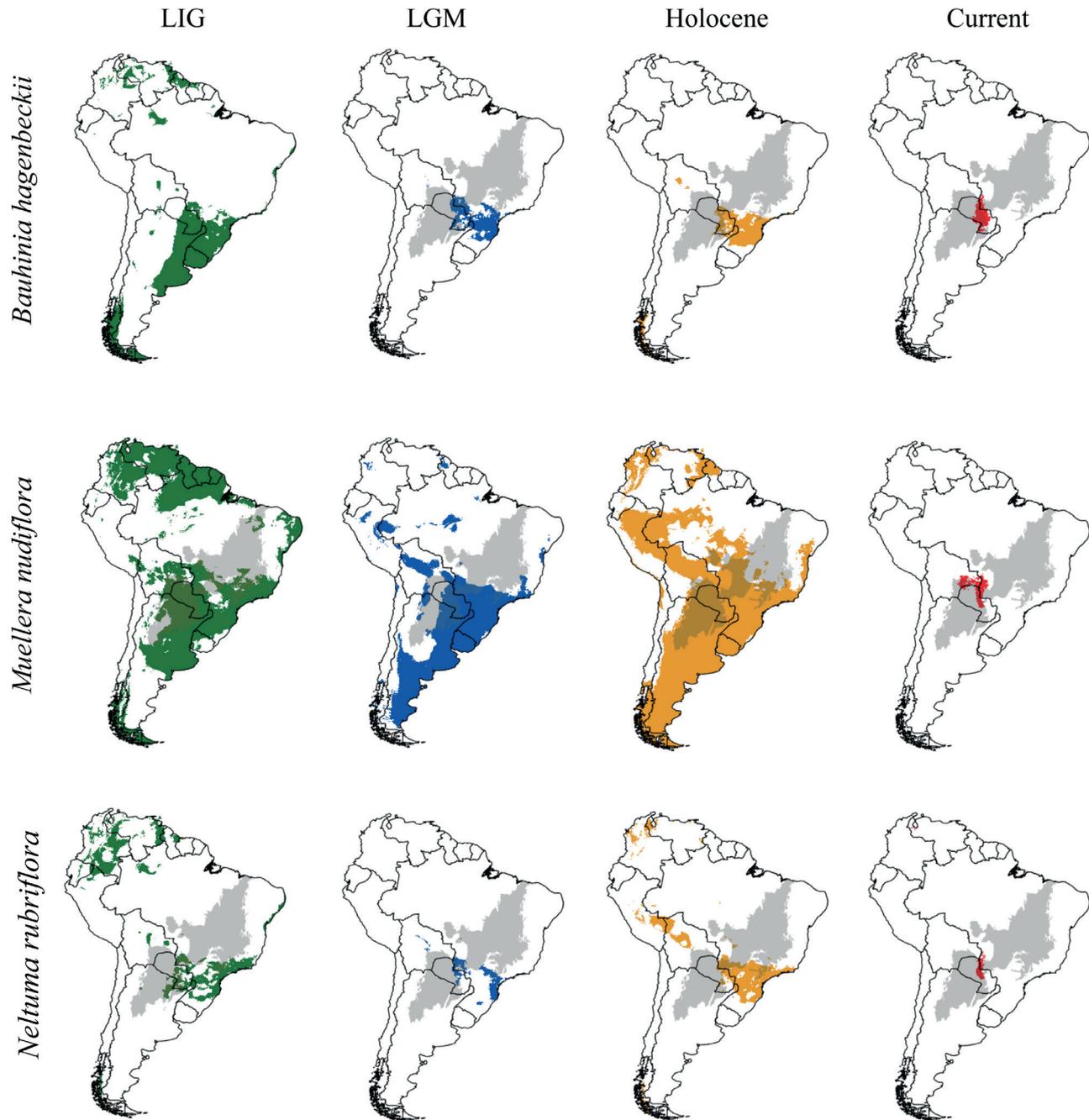


Figure 2. Models of the distribution of *Bauhinia hagenbeckii* Harms, *Muelleria nudiflora* (Burkart) M.J. Silva & A.M.G. Azevedo and *Neltuma rubriflora* (Hassl.) C.E.Hughes & G.P.Lewis in the Chaco and Cerrado, Last Interglacial Maximum (LIG) (green), Late Middle Glacial (LGM) (blue), Holocene (yellow), and WorldClim 2.0 (red) at present.

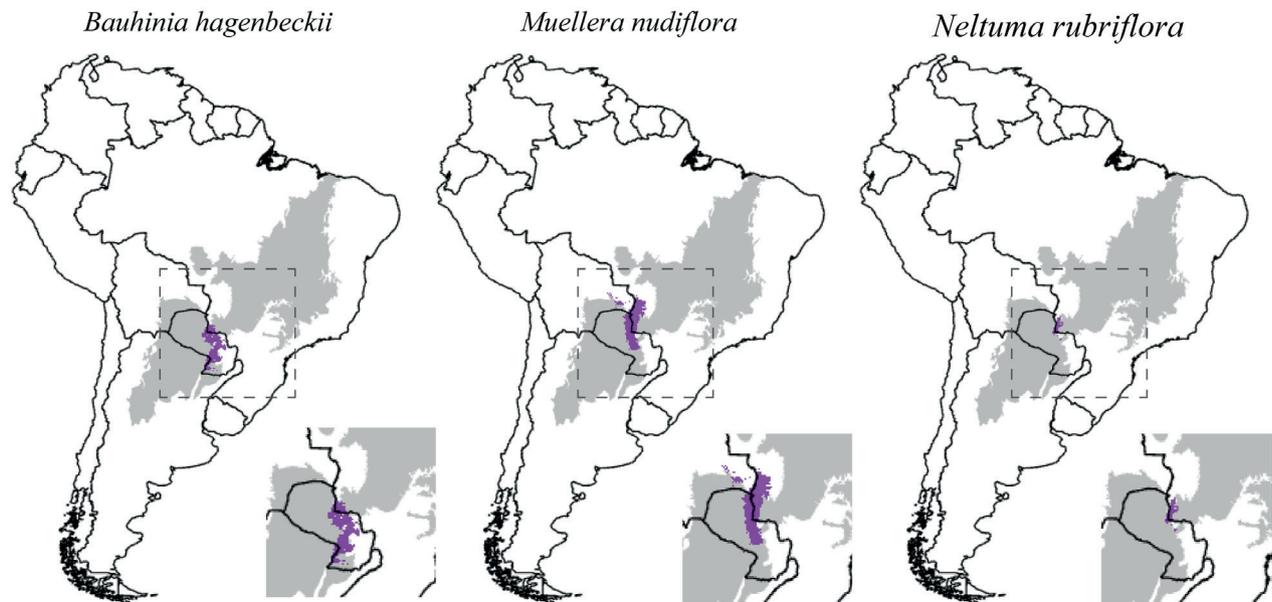


Figure 3. The overlapping of the areas of environmental suitability indicating the stable areas of the four periods, Last Interglacial Maximum (LGM), Late Middle Glacial (LGM), Holocene, and at present of *Bauhinia hagenbeckii*, *Muellera nudiflora* and *Neltuma rubriflora*.

areas from other periods (Figs. 1, 2, 3). During the LIG, the areas of environmental suitability were separated mainly in two wide areas in the southern and northern. LGM models suggest larger areas than those of other times, suggesting areas of environmental suitability in Colombia, Guiana, Peru, coastal Chile, the central area of Bolivia and Paraguay, in the Northeast, Central-West, Southeast and South regions of Brazil, in Uruguay, and in southern Argentina. Models for the past three periods suggest discontinuous areas in some regions of Peru, Chile and Argentina. Models for the present time suggest areas of environmental suitability in the Chacoan region of Bolivia, Paraguay and Brazil.

The models of *N. rubriflora* (Figs. 1, 2, 3) suggested similar areas of environmental suitability when compared to *B. hagenbeckii*. LIG's environmental suitability areas have shown possibilities in Colombia, Ecuador, Venezuela, Guiana and Suriname, and other disjoint areas in Paraguay, Bolivia, Argentina and Brazil. The model suggests larger areas during the Holocene period than during the LIG period in central Bolivia, southeast Peru and in the Central-West, Southeast and South regions of Brazil. For the present time there are models indicating a reduction in the areas of environmental suitability compared to past times, suggesting this endemic situation to the Paraguayan and Brazilian Chaco.

The overlapping of the areas with environmental suitability of the four periods, LIG, LGM, HM and present (Fig. 3), indicate that there is a small area of overlap, that is, refuge areas suggesting that climatic variations can cause a total loss of the environments for *B. hagenbeckii*, *M. nudiflora* and *N. rubriflora*. It is also important to point out that the distribution of the species *B. hagenbeckii* and *M. nudiflora* should be carefully monitored since the refuge areas suggest a process of extinction in the near future.

Discussion

Climatic fluctuations of the Quaternary were determinant and consistent regarding the distribution of the three species, demonstrating cycles of retraction and expansion in the scenarios analysed. Climate variability as demonstrated by paleoclimatic and paleoenvironmental studies (Bissa *et al.* 2013; Correa-Metrio 2014; Arruda *et al.* 2018; Blonder *et al.* 2018; Vale & Pires 2018) suggests that the proposed variations in the HM, LGM and LIG models are possible regarding environmental suitability.

Areas with a high probability of occurrence were pointed out by the models due to the fact that climatic conditions were similar to those of the occurrence records. Thus, temperature and humidity were the main climatic factors altered during the past periods, as also reported in other studies (Urrego *et al.* 2016; Oliveira-Jr. *et al.* 2017; Arruda *et al.* 2018). However, some extrapolations of the models include potential areas exceeding the known distribution of the selected species even at present, without considering geographical and pedological barriers (Nascimento *et al.* 2013; Arruda *et al.* 2018).

The largest and fragmented expansion in the Last Interglacial (LIG) (Otto-Bliesner *et al.* 2006) of suitable areas of the analysed species coincided with the expansion of suitable areas in the north-eastern and southern regions of South America and along the coast of Brazil. The fragmentation of suitable habitats in the LIG is expected, given that a warmer and wetter climate is more suitable for forest expansion (Otto-Bliesner *et al.* 2006). This is due to the fact that the species analysed occur in the wet areas of the Chaco in Paraguay and Brazil (Wunderlin 1968; Burkart



& Simpson 1977; Souza-Lima *et al.* 2017). Consequently, *Bauhinia hagenbeckii* and *Prosopis rubriflora*, following this expansion, fragmented mainly in the north-western and southern regions of South America and along the coast of Brazil, considered regions of higher wetness during the LIG (Carnaval & Moritz 2008; Carnaval *et al.* 2009; Cheng *et al.* 2013; Carnaval *et al.* 2014). On the other hand, *Muellera nudiflora* occurred mainly in larger areas of the northwestern region of South America, which is considered to have had higher humidity and climatic stability over the Quaternary (Colinvaux & De Oliveira 2000).

In contrast, in the LGM model, suitable areas retracted toward their current areas of occurrence, with a general picture of cooler temperatures and greater aridity in almost every region of South America (Markgraf 1993; Clapperton 1993). Rainfall is considered a key ecological factor for determining the distribution of taxa in the Chaco (Rezende *et al.* 2020). Thus, it is evident that changes in this variable in the past, as the supposed increase in aridity during the periods of Pleistocene glaciers (Zanella 2011), must have resulted in modifications of its distribution pattern. In addition, a dry, sparse tundra was present in the southern region of South America and the Andean temperate forest was reduced to scattered remnants on the western side of the Cordillera (Markgraf 1993). However, some species that commonly occur in the Brazilian Pantanal, such as *Mauritia flexuosa* and *Tabebuia aurea*, were reduced in the present environmental suitability areas in relation to the LGM (Sciamarelli & Torgeski 2019) possibly due to favourable environments for the expanded occurrence of the two species throughout the Pantanal and Chaco. Also, *Monttea aphylla* (Plantaginaceae), an endemic plant of Argentina, showed variations during the glacial periods of the past, and in the present the areas of environmental suitability should be larger (Baranzelli *et al.* 2017), whereas in fact, during the LGM there was a drastic retraction in the occurrence of tropical forests (Bush & Silman 2004; Carnaval *et al.* 2009; 2014). Genetic analysis of populations and distribution modelling of *Tabebuia roseoalba*, in South America, have suggested that their distribution during the LGM may have been lower than during warmer periods and during the LIG, HM and present (Melo *et al.* 2016). These variations of the distribution models of the studied species over the different periods showed the same behaviour as the areas of environmental suitability.

According to Iriondo & Garcia (1993), the climate may also have remained in a relatively cold, arid mode compared to its later Holocene state, with desert-like conditions in the Chaco region. Thus, the general temperatures resembled those of the present day, only slightly cooler (global annual cooling less than -0.1°C), with more significant changes recorded regionally and seasonally (Otto-Bliesner *et al.* 2006).

There is evidence of complexity in the evolutionary history of South American deserts. A comparative

phylogeographic analysis was carried out in a plant community in the southernmost areas of Diagonal Arid South America, providing relevant information for the preservation of the Chaco, suggesting which species to study that may have been affected by variations in abiotic factors and in the intrinsic characteristics of plant populations (Baranzelli *et al.* 2020).

The final climate switch to 'optimum' conditions for the occurrence of the species analysed (the moistest and warmest) may have occurred at around 8,000 BP and may have lasted until about 5,000 BP, after which there was a return to rather arid conditions. However, according to Prieto (1996), the initial switch to moister-than-present conditions in the region and elsewhere began considerably earlier, at the start of the Holocene. In the extreme south, the temperate evergreen forests had returned on the western side of the Andes but had not yet spread through the eastern side (Markgraf 1993).

Bauhinia hagenbeckii, with current distribution in both Chaco and Cerrado, should be related to variations of vegetation formations (Zanella 2011; Arruda *et al.* 2015; 2018; Bueno *et al.* 2017). According to Arruda *et al.* (2018), vegetation formations are not altered by climatic variations alone, but rather by joint climate and soil actions. The occurrence of *B. hagenbeckii* was always associated with the typical Chaco areas (Vaz & Tozzi 2005, Sartori *et al.* 2018, Morales *et al.* 2019). There are gaps in the records of *B. hagenbeckii* occurrence in Paraguay, a fact that requires a larger sampling effort in data collection for this species.

The restricted occurrence of *N. rubriflora* suggests its endemism for the Chaco (Fig. 3), an aspect already reported by Morales *et al.* (2019). It is worth mentioning that the occurrence of *Neltuma rubriflora*, like that of *Muellera nudiflora* and *Bauhinia hagenbeckii*, is restricted to the Chaco region. However, it would be interesting if collections were planned according to the guidelines suggested by the models regarding *Neltuma rubriflora*. It is worth mentioning that there are no records of this species for Bolivia in some herbaria and in others the collections have not yet been digitized.

Recent studies have revealed the impact of climatic oscillations (*e.g.* glacial/interglacial cycles, sea level changes) as a driver of speciation and distribution in Solanaceae and Passifloraceae grassland species of the Pampa and Chaco domains (Moreno *et al.* 2018; Köhler *et al.* 2020). Other species that occur in the Pampas and Chaco region such as *Petunia*, showed similar results mainly in the LGM and HM, highlighting areas of environmental suitability larger than at present in a study of phylogeography and modeling (Giudicelli *et al.* 2019).

Temperature and precipitation may be the determining factors for the distribution patterns of Chaco species (Rezende *et al.* 2017; 2018). Thus, it was possible to delimit refuge areas according to the patterns of suitability areas for the species. Since there is a lack of priority preservation



in the whole Chaco, the overlapping of models during the different periods studied suggests that species may totally lose the environments favourable to their existence by losing areas that they could explore, also because these areas have been explored in agro-pastoral activities over recent decades.

The present distribution of the Leguminosae species of this study is related to the climatic events of the Quaternary, based on retraction and expansion. All the models of the scenarios (Last Interglacial, Last Glacial Maximum, Medium Holocene and the current scenarios) highlighted the potential distribution of these species concomitant with the events of glacier regression and were consistent with the history of the formation of the dry areas of South America. The present potential distribution of the legumes of this study is consistent with the history of the Dry Diagonal formation (Werneck *et al.* 2011).

A phylogenetic study highlighted that Leguminosae species tolerate drier regions, explaining their dominance. For this reason, the group may be increasingly important in the restoration of the Chaco vegetation (Maza-Villalobos *et al.* 2020). The present study and others suggest that environmental conditions during past periods may justify certain current distributions of plant species in South America.

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