

The fate of *Holoregmia*, a monospecific genus endemic to the Brazilian Caatinga, under different future climate scenarios

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Abstract

Background and aims – Climatic fluctuations during the Pleistocene altered the distribution of many species and even entire biomes, allowing some species to increase their range while others underwent reductions. Recent and ongoing anthropogenic climate change is altering climatic patterns very rapidly and is likely to impact species' distributions over shorter timescales than previous natural fluctuations. Therefore, we aimed to understand how Pleistocene and Holocene climatic fluctuations might have shaped the current distribution of *Holoregmia* and explore its expected distribution under future climate scenarios.

Material and methods – We modelled the potential distribution of *Holoregmia viscida* (Martyniaceae), a monospecific plant genus endemic to the semi-arid Caatinga Domain in Brazil. We used an ensemble approach to model suitable areas for *Holoregmia* under present conditions, Paleoclimatic scenarios, and global warming scenarios in 2050 and 2090.

Key results – Holocene climates in most Caatinga were too humid for *Holoregmia*, which restricted its suitable areas to the southern Caatinga, similar to its current distribution. However, under global warming scenarios, the Caatinga is expected to become too dry for this lineage, resulting in a steady decline in the area suitable for *Holoregmia* and even its possible extinction under the most pessimistic scenario modelled.

Conclusion – The predicted extinction of the ancient and highly specialized *Holoregmia viscida* highlights the possible consequences of climate change for some species of endemic Caatinga flora. Invaluable phylogenetic diversity may be lost in the coming decades, representing millions of years of unique evolutionary history and consequent loss of evolutionary potential to adapt to future environmental changes in semi-arid environments.

Keywords

biogeographic distribution, biological conservation, Brazilian semi-arid region, ecological niche modelling, *Holoregmia viscida*, ENMTML

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INTRODUCTION

Climate has long been considered a major determinant of species and vegetation distribution (Adams 2010). This intricate connection between climate and the biota underlies influential hypotheses regarding bioregionalization and diversification. In particular, alternation between glacial and interglacial periods of the Pleistocene played a key role in shaping current patterns of species and biome distribution (Buono et al. 2017; Costa et al. 2017; Ledo and Colli 2017; Buzatti et al. 2018).

Species distribution is strongly linked to the combination of factors and conditions that allow their survival and reproduction (Hutchinson 1957). The history of biogeography itself is related to understanding latitudinal and altitudinal gradients of habitats and species following climate (Lomolino et al. 2004). The climate is one of the main variables responsible for modifying the patterns of species occurrence in the world, resulting in the complex species distributions of the global biota (Hewitt 2000).

Although climate has varied dramatically over Earth's history, current climate change is an increasingly accelerated human-induced process. Increased emissions of greenhouse gases in recent decades are likely to cause a substantial impact on biodiversity (IPCC 2001, 2007; Garcia et al. 2014). In addition, effects on the geographic species distribution, phenological and physiological processes have been predicted to occur (Walther et al. 2002; Bellard et al. 2012; Shrestha and Bawa 2014) and, more recently, documented. For example, Lima et al. (2021) evaluated the reproductive phenological changes of four species of Melastomataceae endemic to the Brazilian Atlantic Forest over almost 100 years, in which the temperature increased continuously and precipitation varied greatly. The authors observed that reproductive phenology is strongly linked to local climatic conditions and detected significant changes in the season as well as in the seasonality of flowering and fruiting of the species. Other studies have shown different climatic change effects on plant phenology in different localities; in recent years, tropical South American species tend to have later flowering (Fava et al. 2019) in contrast to tropical China species that have flowered earlier over the years (Mo et al. 2017).

Velazco et al. (2020) evaluate the effectiveness of the neotropical region protected area network to protect the phylogenetic diversity of palm trees. Models suggest that in future conditions significant losses in phylogenetic diversity within protected areas are expected, especially if species dispersion is limited. However, even considering more optimistic climatic and dispersal scenarios, protected areas remain ineffective for protecting the phylogenetic diversity of palm trees in the current climate and will continue in the future. The authors point out that the expansion of areas and conservation strategies could improve the conservation of the phylogenetic diversity of palm trees. Ultimately, predicted climate changes may

be responsible for the extinction of many species in the coming years (Thomas et al. 2004).

Much of the public concern about the consequences of climate change on biodiversity is related to the tropical rainforest biota. But across the tropics, there are many areas under semi-arid climate bearing seasonally dry tropical forests and woodlands (Pennington et al. 2000; Queiroz et al. 2017), which harbour endemic lineages adapted to seasonal climates. Some future scenarios indicate that semi-arid and arid environments are especially vulnerable to climate change (IPCC 2007). The Caatinga Domain is a semi-arid system considered one of the ecosystems with the greatest sensitivity to climate change (Seddon et al. 2016). If the climate changes permanently, this will affect the ecological niche of species in this environment (e.g. Chagas et al. 2020; Silva et al. 2020; Simões et al. 2020).

Encompassing more than 3,300 flowering plant species, including 29 endemic genera (Fernandes et al. 2020), the Brazilian Caatinga is the most diverse nucleus of the neotropical Seasonally Dry Tropical Forest biome (SDTF) (Dryflor et al. 2016; Queiroz et al. 2017; Fernandes et al. 2020). The high morphological divergence of SDTF endemic genera suggests that they represent ancient lineages (Pennington et al. 2006). Thus, their potential local or global extinction due to predicted reductions in the suitable habitat areas for endemic species (e.g. Silva et al. 2019) would mean the loss of a considerable amount of invaluable phylogenetic diversity.

Due to the centuries-long efforts of biological collections to preserve botanical records and more recent initiatives to increase their accessibility through digitization (Canteiro et al. 2019), an unprecedented volume of data is now available for taxonomy, evolution, ecology, and conservation studies (Harley et al. 2003; Gormley et al. 2015; Queiroz et al. 2017; Canteiro et al. 2021). Here, we advance knowledge of the recently rediscovered Caatinga endemic genus *Holoregmia*. Thus, our objective was to compile information from collections to document the current distribution of *Holoregmia viscida*, a clade endemic to the semi-arid Caatinga in Brazil. To understand how it reached its current distribution, we modelled the species niche under paleoclimatic conditions. We also aimed to understand the possible impact of climate change on the potential distribution of this species and evaluate if it is likely to be threatened by global warming. Finally, considering the different modelling scenarios, we assume that the species' fundamental niche is conserved over time and space (Peterson 1999).

MATERIAL AND METHODS

Study species

Holoregmia Nees (Martyniaceae), a monospecific genus is an iconic example of Caatinga's ancient endemic genera. First collected by Prince Maximilian of Wied in 1817 and formally described by Nees in 1821 (Nees

1821), *Holoregmia viscida* is a robustly branched shrub attaining a height of up to 3 m (Harley et al. 2003), thus unlikely to be overlooked by botanical collectors in the field. However, due to the incomplete and fragmentary nature of the original material, the correct application of the name *Holoregmia* and the distinctive nature of this monotypic genus remained in doubt until the early 21st century. Late 19th century authors considered *Holoregmia* doubtfully distinct as a genus and probably a synonym of *Craniolaria* L. A revision of the Martyniaceae by Van Eseltine in 1929 (Van Eseltine 1929) omitted *Holoregmia* entirely, reflecting the lack of information about this Caatinga endemic genus (Harley et al. 2003).

Although documentation of the Brazilian flora advanced rapidly in the second half of the 20th century (Forzza et al. 2010; Morim and Nic Lughadha 2015), specimens of *H. viscida* collected at that time were often mistakenly identified under other botanical families or left unidentified among the Martyniaceae family specimens, including several collections from the 1980s onward deposited in the HUEFS herbarium (Universidade Estadual de Feira de Santana), which is now reported to have the largest collection of *H. viscida* species in Brazil (Giulietti and Harley 2013). The lack of accessible, complete, and authoritatively identified reference material in herbaria prevented the recognition of this peculiar genus as a distinct endemic genus. However, new field collections in the early 21st century were finally recognized

as *Holoregmia*, prompting a review of unidentified plant material in herbaria, including the 1980s collections, resulting in a detailed morphological description of this monospecific genus (Harley et al. 2003).

Holoregmia viscida has long racemes of zygomorphic flowers borne well above the leaves. The calyx is foliaceous, pale green; the tubular corolla is fleshy, dull-yellow mottled with brown and darker at the throat. The two stamens bear cream anthers, and the stigma is prominent (Fig. 1). The fruit is a rounded, two-seeded capsule. The plant becomes dormant during dry periods, sprouting with the first rains. It can be found flowering between October and April, fruiting from January to August (Sinzinando Albuquerque and Daniela Zappi pers. comm.). No direct observations concerning pollination are available, but pollination by large bees has been suggested as probable (Harley et al. 2003). The same authors observed that a trait considered typical of Martyniaceae, a pair of horns borne at the apex of the endocarp, is almost imperceptible in *Holoregmia*, leading to the conclusion that the fruit morphology does not suggest epizoochory, which is characteristic of other family members.

Occurrence records and data cleaning

We searched digital biological databases for records of *Holoregmia viscida* both under its current name and under the synonyms *Craniolaria unibracteata* Nees &

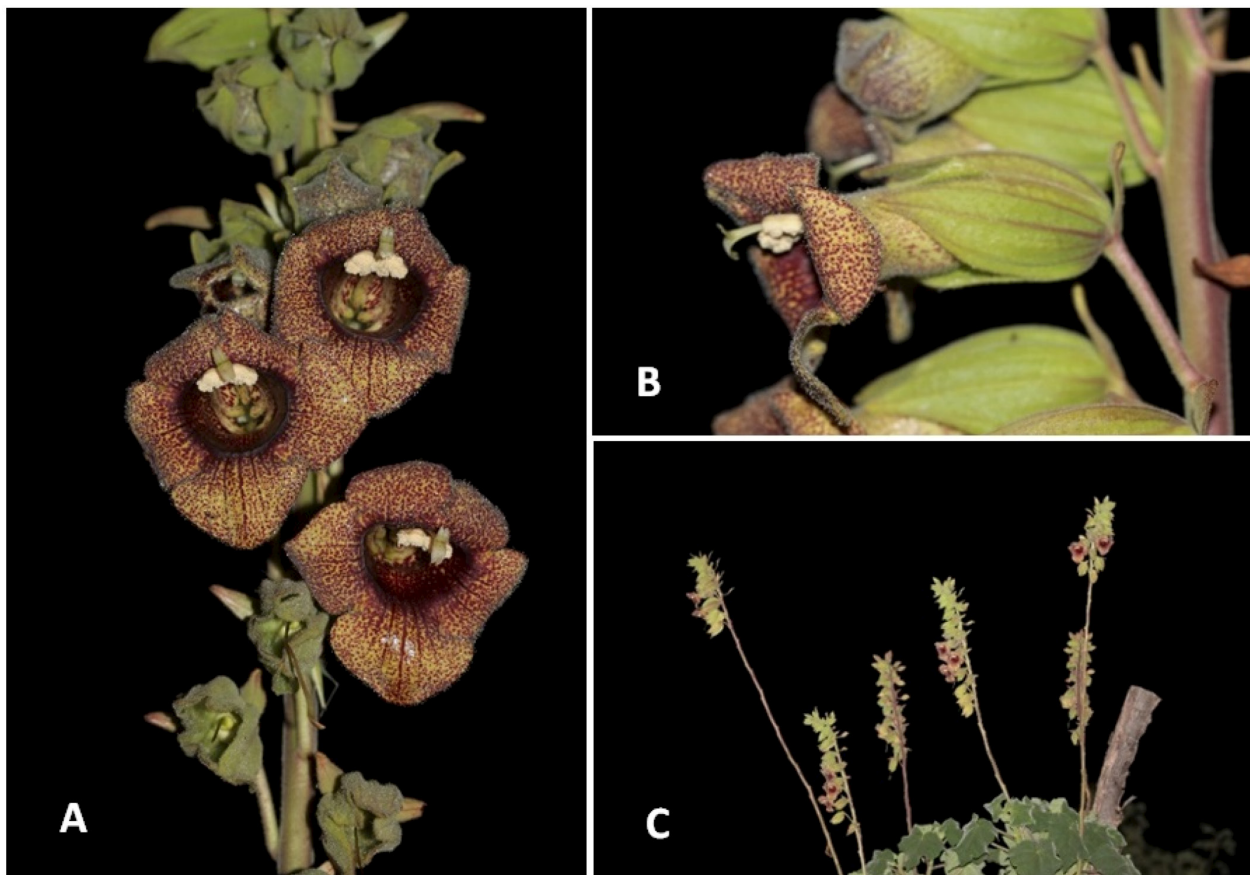


Figure 1. *Holoregmia viscida* Nees showing its inflorescences and details of the flowers. Photos by Sinzinando Albuquerque.

Mart., *Martynia spathacea* Spreng. and *Proboscidea unibracteata* (Nees & Mart.) Decne. referenced in Flora e Funga do Brasil (Rossini and Gonzaga 2020 – <https://floradobrasil.jbrj.gov.br/FB25778>, data collected in June 2021) and Plants of the World Online (Govaerts et al. 2021 – <https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:327210-2>, data collected in June 2021). We obtained 41 occurrence records for *Holoregmia viscida* from the Brazilian databases Species Link (<https://sblink.cria.org.br/>, data collected in June 2021), Reflora Virtual Herbarium (<http://reflora.jbrj.gov.br/reflora/herbarioVirtual/>, data collected in June 2021), and the international database Global Biodiversity Information Facility (<http://www.gbif.org/>, data collected in June 2021). We checked the taxonomic identification for each of these records by consulting the relevant specimens in the Herbarium of the State University of Feira de Santana (HUEFS), which houses most of these collections, or examining digital images available in the above-named digital collections. Records were cleaned for geographic errors using the R package CoordinateCleaner v.2.0-20 (Zizka et al. 2019) and corrected for spatial sampling bias using the R package spThin v.0.2.0 (Aiello-Lammens et al. 2015). Our final dataset included a total of 34 georeferenced, taxonomically validated records (Supplementary file 1).

Environmental data

To model the potential niche of *H. viscida*, we used 20 variables as predictors for current and future conditions. Of these, 19 were bioclimatic layers of temperature and precipitation, obtained from WorldClim 2.1 (Fick and Hijmans 2017; <http://www.worldclim.org/>) and one was the elevation variable, obtained from NASA Shuttle Radar Topographic Mission (SRTM; <https://lpdaac.usgs.gov/products/srtmgl1v003/>) with 5 arc-min ($0.083^\circ \approx 10$ km) resolution for South America. For the projection of the climatic niche in paleoclimatic scenarios, we used 19 bioclimatic variables obtained from the PaleoClim database (Brown et al. 2018; <http://www.paleoclim.org/>), and to project future global climate change scenarios, we used the models available in the WorldClim database.

We performed a principal component analysis (PCA) on the current environmental variables based on a correlation matrix to overcome multicollinearity problems and reduce the number of predictor variables (Velazco et al. 2019), avoiding model overfitting that may result in biologically unreliable areas (Jiménez-Valverde et al. 2011). We used the criterion that explains at least 95% of the total variance of the correlation matrix and includes as much environmental information as possible (De Marco and Nóbrega 2018; Destro et al. 2019). Thus, the first six axes derived from the PCA were the new set of variables (Supplementary files 2, 3). Then, we used the PCA's eigenvectors to calculate scores of each derived PC as new predictors (Velazco et al. 2019).

For paleoclimatic projection, we selected three scenarios: Last Interglacial (ca 130 ka), Last Glacial Maximum (ca 21 ka), and Mid-Holocene (8.326–4.2 ka). We did not include the elevation variable in the paleoclimatic projection. To model future climatic scenarios, we used the climate projection from the Intergovernmental Panel on Climate Change (AR6) as the source of future climate conditions. We evaluated the effect of climate change using three Shared Socioeconomic Pathways (SSPs) based on Coupled Model Intercomparison Project Phase 6 (CMIP6). We selected three scenarios: SSP126 is the updated scenario of RCP2.6, which is an optimistic scenario that would occur in a sustainable world that takes a green path with low greenhouse gas emissions; SSP245 is the updated RCP4.5 scenario that uses an intermediate level of greenhouse gas emissions; and SSP585 is the updated scenario of RCP8.5, which is the most pessimistic and assumes that use of fossil fuels will continue to increase (O'Neill et al. 2014, 2017) forcing a high level of greenhouse gas emissions (Gillett et al. 2016). We used projections for 2050 (mean for the period from 2041 to 2060) and 2090 (mean from 2081 to 2100) using the General Circulation Model IPSL-CM6A-LR.

Ecological niche models

Ecological niche models (ENMs) are empirical or mathematical approximations of the ecological niche of a species (Barbosa et al. 2012). Based on different statistical approaches, a plethora of algorithms are available to predict the niche of a species (Velazco et al. 2021). Based on the occurrence records of the target species associated with the set of climatic variables, the algorithms create a multidimensional environmental space that infers the niche of the species (Araújo and Guisan 2006; Carvalho et al. 2017). Species occurrence records can present possible errors and biases in the data, so it is important to clean and filter the data (Zurell et al. 2020). However, algorithms are the primary sources of uncertainty in the models. Thus, testing the effect of different algorithms on modelling is essential to detect the best model (Thuiller et al. 2019). We adopted a routine with six different algorithms to evaluate niche modelling (Supplementary file 4): i) Bioclimatic Envelope Method (Booth et al. 2014); ii) Maxent, with default features – MaxNet (Phillips et al. 2006, 2017); iii) Simple Maxent Model (Williams 2010); iv) Support Vector Machine (Tax and Duin 2004); v) Random Forest – RDF (Breiman 2001); and vi) Gaussian Model (Golding and Purse 2016) (see individual models in Supplementary file 5).

We tested the performance of our ecological niche modelling using spatial block cross-validation, based on a geographically structured checkerboard to control the potential spatial autocorrelation between training and testing data (Roberts et al. 2017). The test and training data were used to test for spatial autocorrelation (Moran's I) and environmental similarity (MESS – Multivariate

Environmental Similarity Surface) (Destro et al. 2020). Moran's I ranges from -1 to 1, distinguishing between negative and positive spatial autocorrelation, respectively (Diniz-Filho et al. 2003). MESS analysis identifies and determines the extent of the environmental differences between model training and model projection (predictions are extrapolations) data (Elith et al. 2010), where the higher the value, the more common the environment of the training point (Camera et al. 2017). Negative values indicate a novel environment, i.e. different environmental locations from the reference region.

Models that use presence-only data are strongly influenced by bias, while models that use presence/pseudo-absence data are not (Phillips et al. 2006). Thus, we selected the method in which pseudo-absences are environmentally constrained to a region with suitability values predicted by a BIOCLIM model (Wisn and Guisan 2009). First, we set the threshold based on the maximization of sensitivity-specificity sum (Liu et al. 2005). Then, an ensemble was created for the species, selecting the best models with True Skill Statistic (TSS) above the average (Marmion et al. 2009; Velazco et al. 2019). We used the Area Under the Curve (AUC) and the True Skill Statistic (TSS) to evaluate the models' accuracy. The AUC is a threshold-independent index, where values of $AUC \geq 0.8$ are considered good to excellent (Komac et al. 2016) to discriminate the places occupied by a species and places where occupation is unknown. The TSS is a threshold-dependent index, where TSS values > 0.6 are considered good to excellent (Komac et al. 2016) and indicate greater agreement between the observed and predicted distribution of the species (Allouche et al. 2006). The models were constructed using the R package ENMTML v.1.0 (Andrade et al. 2020). We established four classes from the threshold set by TSS, ranging from 0 to TSS; TSS to 0.60; 0.61 to 0.80; 0.81 to 1. We also calculate the area suitable for each scenario from the threshold. Our ENM were generated projecting the niche to the Neotropics (all models are available for download in our supplementary data). We calculated suitable areas for the species within the Brazilian territory and for South America. Those interested in the result for the entire continent can recalculate the data using the rasters available for download.

RESULTS

Mapping the distribution of all records of *Holoregmia viscida* confirmed that it is an endemic species restricted to the southern part of the Caatinga Domain. Furthermore, this pattern shows that this species is mainly associated with the lowlands of the Depressão Sertaneja Meridional lowlands of the Caatinga and the surrounding highlands scattered across the Depressão Sertaneja and Chapada Diamantina (Fig. 2).

Model performance

For paleoclimate scenarios, the ensemble model showed a satisfactory performance with AUC 0.95 with a standard deviation of ± 0.06 , and TSS values of 0.84 with a standard deviation of ± 0.2 (Supplementary file 6). For the climate change scenarios, the ensemble model showed a satisfactory performance with AUC 0.92 with a standard deviation of ± 0.005 and TSS values 0.81 with a standard deviation of ± 0.06 (Supplementary file 6). Moran's I values for paleoclimate and climate change scenarios were 0.008 and 0.033 (Supplementary file 7), respectively, indicating low spatial autocorrelation of environmental variables. All values were positive, indicating that the training-test subregions presented similar environments, i.e. they do not suffer from induced low precision due to subsets of data being in climate-discrete regions or questions related to model extrapolation (Peterson et al. 2007; Owens et al. 2013).

Paleoclimate scenario simulation and current climate

The suitable areas for the occurrence of *Holoregmia viscida* have oscillated in paleoclimatic scenarios. Our results showed that the appropriate environmental conditions during the Last Interglacial were distributed mainly in the Atlantic Forest Domain and to a lesser extent in the south of the Caatinga, resulting in an area of 135,919 km² for Brazil and 212,612 km² for South America (Fig. 3). These suitable areas for the occurrence of *H. viscida* increased to 198,488 km² for Brazil and 273,621 km² for South America in the Last Glacial Maximum. They were displaced within the boundaries of the Caatinga Domain with small areas in the Cerrado Domain (Fig. 3). In the Mid-Holocene, the geographical extent of suitable areas was reduced to 82,394 km² for Brazil and 153,971 km² for South America, becoming restricted to the south of the Caatinga Domain (Fig. 3). Thus, the adequate areas during the Holocene were likely limited, representing a fraction of *Holoregmia*'s current total suitable area. This loss explains why *Holoregmia* is now limited to the southern Caatinga, even though suitable areas are also found in parts of the northern Caatinga (Fig. 3). For the current climate conditions, the models estimated an area of 156,372 km² for Brazil and 215,953 km² for South America that includes the regions with the highest suitability for the occurrence of *Holoregmia viscida*. The focus of all maps in Fig. 3 is centered in the Caatinga dry forests, but climatically suitable areas for *H. viscida* can also be found outside this frame. Full data for all models is available as raster files on Figshare scientific repository (see Data Availability Statement).

Climate change scenario simulation

The species' niche will be affected by future climatic conditions, even under the most optimistic scenarios

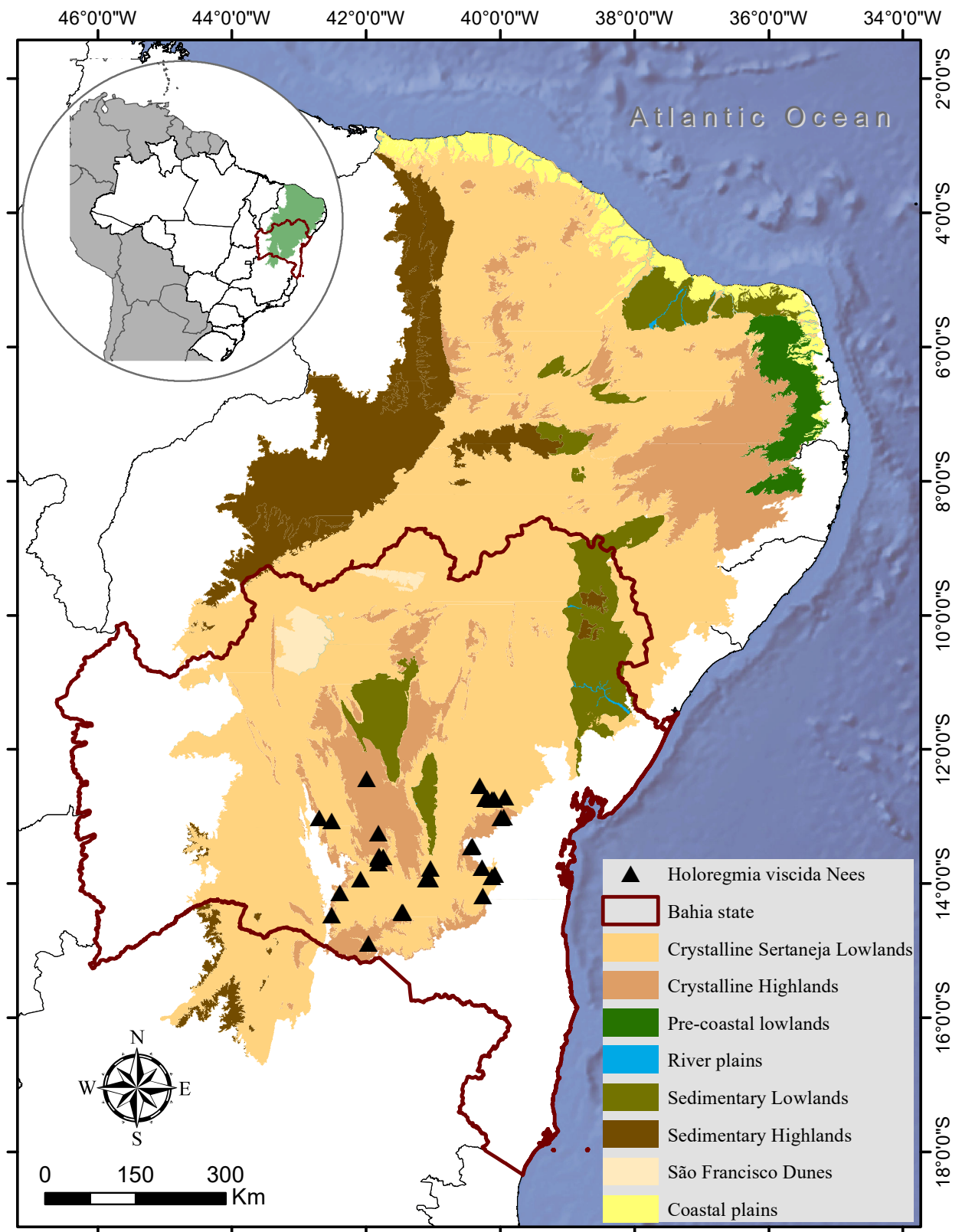


Figure 2. Spatial distribution of taxonomically validated records of *Holoregmia viscida* (Martyniaceae). The inset shows the extent of the Caatinga in South America as proposed by IBGE (2019), while the main map shows the Caatinga with its main geomorphologies. Note that *H. viscida* is restricted to the southern part of the lowlands of the crystalline landscapes of the Depressão Sertaneja and a few associated highlands.

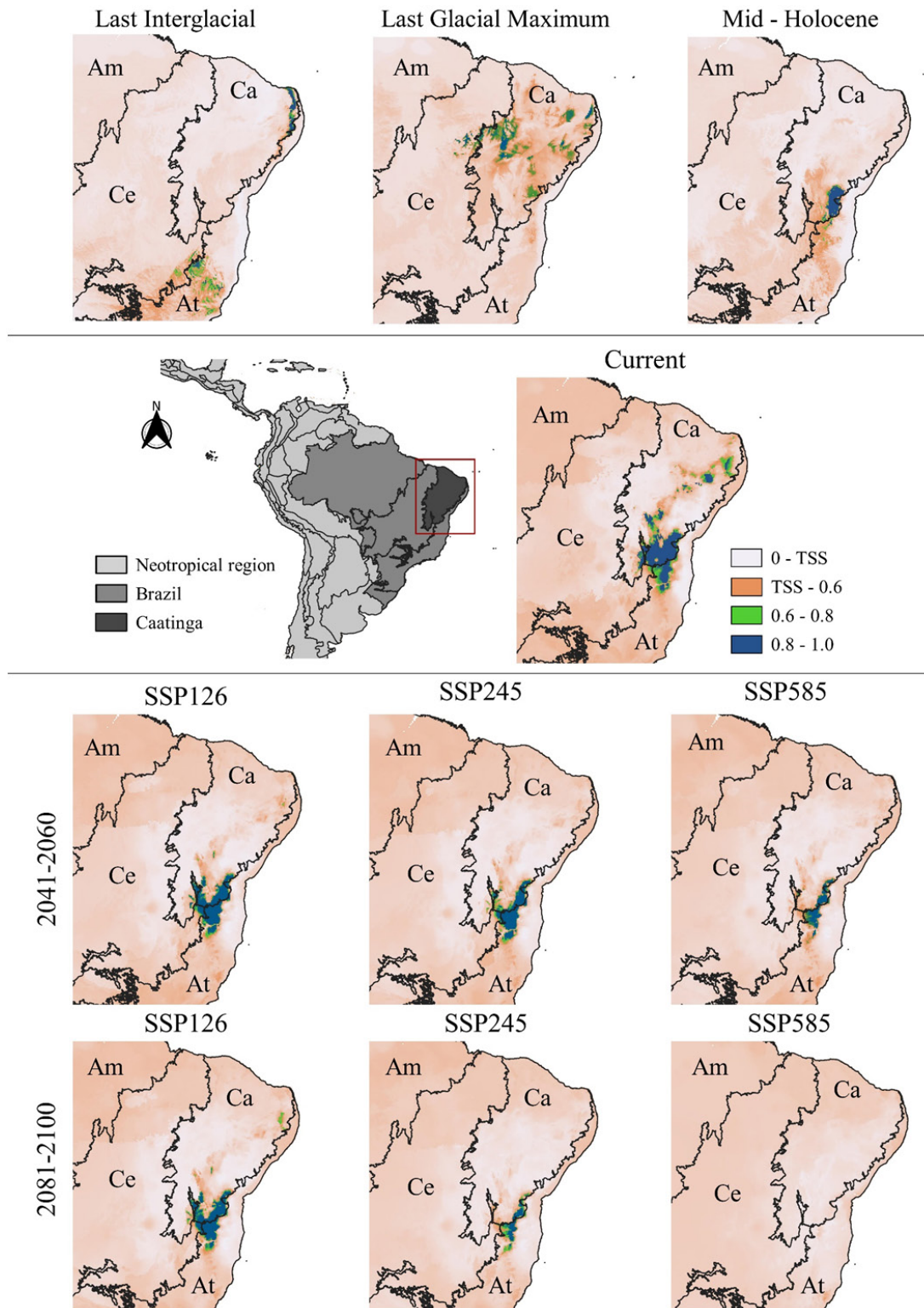


Figure 3. Map zooming in the Caatinga Domain showing the climatic suitability for *Holoregmia viscida* in current conditions (centre of the figure), paleoclimatic scenarios (top of the figure) and three future climate change scenarios (bottom of the figure). Brazilian phytogeographical domains: Am – Amazon Rainforest; At – Atlantic Rainforest; Ca – Caatinga; Ce – Cerrado. TSS represents the True Skill Statistic, used to define the best model and the threshold value in the model to decide whether a pixel has suitable conditions for the occurrence of the species. SSPs are the Shared Socioeconomic Pathways, which are possible scenarios regarding the future emission of greenhouse gases. The SSP126 is an optimistic scenario that would occur in a sustainable world with low greenhouse gas emissions; SSP245 considers an intermediate level of greenhouse gas emissions; and SSP585 is the most pessimistic scenario and assumes that the use of fossil fuels will continue to increase.

(Fig. 3). The SSP126 scenario predicts that the niche will be reduced to 84,928 km² for Brazil (i.e. 54.31% of the current range) and 109,124 km² for South America (i.e. 50.53% of the current range) in 2050 and 79,418 km² (i.e. 50.78% of the current range) for Brazil and 99,909 km² for South America (i.e. 46.26% of the current range) in 2090. Niche losses tend to increase under the SSP245 scenario, with an average reduction to 67,248 km² (i.e. 43% of the current range) for Brazil and 83,522 km² (i.e. 38.67% of the current range) for South America in 2050 and 30,309 km² (i.e. 19.38% of the current range) for Brazil and 37,262 km² (i.e. 17.25% of the current range) for South America in 2090. The SSP585 scenario estimates more significant niche losses than the other scenarios, reducing to 37,274 km² (i.e. 23.83% of the current range) for Brazil and 51,151 km² (23.68% of the current range) for South America in 2050 and a total loss in 2090 for Brazil and 1,341 km² (i.e. 0.62% of the current range) for South America. Under this latter scenario, it is possible that *H. viscida* will become extinct, as no suitable areas will remain (Fig. 3).

DISCUSSION

Past, present, and future of *Holoregmia viscida* in the Caatinga

Martyniaceae is a New World family primarily associated with dry ecosystems (Gormley et al. 2015), suggesting the lineages conserve their niche adapted to dry areas. Considering that *H. viscida* is estimated to have diverged from its sister taxa 9.4 million years ago (Queiroz et al. 2017), this lineage has undoubtedly been subjected to multiple climatic fluctuations throughout its evolutionary history. Currently, the genus is limited to the southern part of the Caatinga. This restricted occurrence is likely the result of the paleoclimatic fluctuations, as discussed below. The potential niche of *H. viscida* appears to have expanded from the Last Interglacial to the Last Glacial Maximum, however, models show a considerable niche loss in the Holocene. In addition, the potential niche in the Holocene was much smaller and restricted compared to the current niche.

In the current scenarios, the potential niche goes beyond the southern Caatinga, since suitable areas are also found in the northern Caatinga today. For future conditions, the effects of climate change on the ecological niche of *H. viscida* may be irreversible. The models showed that the species tends to lose suitable areas in optimistic scenarios and especially in pessimistic scenarios, with the possible extinction of the species in SSP585 by the year 2100.

Paleoclimate scenario models

Our paleoecological reconstructions show a major displacement of *H. viscida* throughout the Quaternary. While in the Last Interglacial (Fig. 3), suitable niches

for the species occurred in the northeastern part of the Caatinga, and also in areas within the Cerrado and the Atlantic Forest Domains; during the Last Glacial Maximum (LGM) (Fig. 3), suitable niches appear to have expanded to almost the entire extent of the Caatinga. The model showed that during the LGM, the suitable niches were within the current limits of the Caatinga. The Mid-Holocene had the smallest projected suitable niches of the paleoclimatic scenarios analysed here. In this case, the potentially suitable niches for the species remained restricted to small patchy areas in the southern Caatinga and ecotonal areas between Caatinga and Atlantic Forest and drier areas of the Atlantic Forest.

During the Mid-Holocene in the Caatinga, climatic conditions were characterized by increased precipitation, which likely affected the range of optimal climatic conditions for the species. For example, pollen records of the genus *Ziziphus* indicate that in the period from 10,000 to 6,000 years before present (BP), there were taxa adapted to high humidity conditions. However, drier conditions are assumed to have occurred between 6,400 and 1,800 BP based on the lack of sediment deposits in this timeframe (Medeiros et al. 2018). Similarly, the vegetation history of the Caatinga based on peat-bog sediments deposited over > 10,000 years showed that during 10,540–6790 BP, there was a warmer and wetter period evidenced by the prevalence of *Mauritia* pollen, with the establishment of current climatic conditions and vegetation patterns after 4535 BP (Oliveira et al. 1999).

Overall, all results show a great variation in the climatic suitability for *H. viscida* since the Last Interglacial. Its niche exhibits alternation between periods of contraction and expansion and shifts in its geographical placement. Events such as this are likely to leave a signature in the phylogenetic and/or phylogeographic patterns of individual taxa (see Hewitt (2004) for a review). There are many determining factors for the ecological niche of a species (Grinnell 1917; Hutchinson 1957), but the scenario presented here could be helpful as an initial hypothesis explaining the current distribution of *H. viscida*. Given the reduction and subsequent expansion of populations from the LGM onwards, we expect that phylogeographical studies will likely show a signature of a recent population bottleneck in *H. viscida*. Such a bottleneck could have severe implications for the adaptation of the species in the face of future climate change scenarios since such events generally reduce species' genetic diversity (Bellard et al. 2012), making them less likely to survive disturbances.

Future scenario models

Our results indicate that all projected future scenarios involving an increase in temperature and a reduction in precipitation would lead to a major decrease in areas that are climatically suitable for the survival of *Holoregmia viscida*. Such a decrease in the species niche is generally accompanied by a shift in its distribution towards more southern latitudes in areas that currently harbour the

Atlantic Rainforest. The worst-case scenario (SSP585 2080–2100) indicates the complete disappearance of suitable climatic conditions for *H. viscida*, suggesting a possible extinction of the species within 80 years.

A shift of Caatinga towards the Atlantic Forest suggests that climatic conditions related to a combination of temperature and precipitation will be even harsher in the future. Similar results, where a shift in the distribution of Caatinga species towards areas that currently encompass wetter habitats have already been reported for other endemic plants (e.g. Silva et al. 2019) and for the iconic and endemic Caatinga cacti (e.g. Simões et al. 2020).

Changes in the limits between Caatinga, Cerrado, and humid forests were detected during past climatic fluctuations (Costa et al. 2017). We can infer a similar situation by observing *Holoregmia*'s potential niche shifting to areas further south than today, reaching areas now occupied by the Atlantic Forest. This suggests that there will be significant changes in the wetter vegetation adjacent to what is now the Caatinga Domain. This pattern is consistent with Wang et al. (2019), who demonstrated that Tropical and Subtropical Moist Broadleaf Forests in neotropical realms would be more vulnerable to climate change in terms of loss in niches. For example, models projecting suitable areas for *Eschweilera tetrapetala*, a tree species endemic to humid forests of the highlands of Bahia, Brazil, predict a strong reduction in suitable areas for the species by 2070 (Menezes et al. 2021).

Therefore, *Holoregmia viscida* models under global warming scenarios indirectly indicate that areas within the Caatinga Domain may become even drier than they currently are. In contrast, wetter areas within the Atlantic Forest may be under drier and seasonal climates, suitable for species from the Caatinga. While shifts in the biome limits and biotas occurred during Pleistocene climatic fluctuations (Costa et al. 2017; Ledo and Colli 2017), anthropogenic climate change is occurring more rapidly than past natural variations. In the past, slow climate changes happened over thousands of years and allowed the migration of many taxa. Now, with rapid changes expected to occur over decades, associated with the severe deforestation and fragmentation to which biomes are already subjected, many species might not be able to migrate. The Caatinga, for example, has already lost half of its area (Brazil 2015; Antongiovanni et al. 2018), and the majority of the Atlantic Forest has been removed (Brazil 2015).

CONCLUSION

To understand how an endemic genus with 9.4 million years of evolutionary history has a limited distribution inside the semi-arid Caatinga in Brazil, we applied a niche modelling approach under paleoclimatic conditions. We also forecast possible scenarios of loss of suitable area for this species under different global warming scenarios, and our results showed that the *Holoregmia viscida* will have

its distribution affected, even under the most optimistic scenarios. Thus, it is possible that *H. viscida* will become extinct under the most pessimistic scenario of climate change (SSP585), because the models show total loss of suitable areas for the species.

Caatinga, like other biomes, is experiencing severe vegetation loss and fragmentation, and the future scenarios are not optimistic when we consider the generalized impacts of climate change. We used distribution records for this remarkable species derived from decades of data deposited in biological collections, illustrating how critical such institutions are for ecological research on biological responses to environmental change. Most herbaria were established to hold material primarily intended for morphological and taxonomic studies. Here, considering the scientific evidence that climate change is a serious global threat, we emphasize that species distribution data associated with environmental variables can be vital to modelling studies that help us understand how climate change can threaten a single species or a set of species in different ecosystems in the world. Such studies also prompt us to reflect on the potential impacts on the whole biota of a unique biome. We also thank Dr. Luis Ricardo Costa and Dr. Rubson Pinheiro Maia for providing the shapefiles of Caatinga geomorphology that we used to produce our map.

DATA AVAILABILITY STATEMENT

All data from this study are available as supplementary files to this article and in the following links:

The occurrence records and R script to run our analyses are available from: <https://doi.org/10.6084/m9.figshare.17122547>

The raster files of the niche models under current climatic conditions are available from: <https://doi.org/10.6084/m9.figshare.17122271>

The raster files with the niche models under paleoclimatic conditions are available from: <https://doi.org/10.6084/m9.figshare.17122523>

The raster files with the niche models under global warming scenarios are available from: <https://doi.org/10.6084/m9.figshare.17122454>

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SUPPLEMENTARY FILES

Supplementary file 1

Records for *Holoregmia viscida* Nees of in the Caatinga Domain (Brazil).

Link: <https://doi.org/10.5091/plecevo.90511.suppl1>

Supplementary file 2

Coefficients of the principal components selected from the principal component analysis performed with data from niche modelling for climate change scenarios.

Link: <https://doi.org/10.5091/plecevo.90511.suppl2>

Supplementary file 3

Coefficients of the principal components selected from the principal component analysis performed with data from niche modelling for paleoclimate scenarios.

Link: <https://doi.org/10.5091/plecevo.90511.suppl3>

Supplementary file 4

Algorithms used to build species distribution models.

Link: <https://doi.org/10.5091/plecevo.90511.suppl4>

Supplementary file 5

Continuous maps of the areas with the areas of greatest suitability predicted by each algorithm for paleoclimatic periods, current climatic conditions, and future climate change scenarios.

Link: <https://doi.org/10.5091/plecevo.90511.suppl5>

Supplementary file 6

TSS and AUC values.

Link: <https://doi.org/10.5091/plecevo.90511.suppl6>

Supplementary file 7

Moran's I index and Multivariate Environmental Similarity Surface.

Link: <https://doi.org/10.5091/plecevo.90511.suppl7>