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Original Paper

Identification of priority areas for *Eschweilera tetrapetala* (Lecythidaceae) conservation in response to climate change

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Abstract
Eschweilera tetrapetala is a tree endemic to Submontane Seasonal Forests in inland Atlantic forest areas of the Chapada Diamantina Mountains, Northeastern Brazil. The effects of climate change on the spatial distribution pattern of that species were investigated to identify priority areas for its conservation. Distribution patterns and population densities were obtained by sampling individuals in ten 200 x 10 m transects, and in thirty additional 10 x 10 m border and interior forest plots. The occurrence data were subjected to Ecological Niche Modelling using Bioclim, Maxent, and Support Vector Machine algorithms. The predicted model for the current distribution of *E. tetrapetala*, using the Bioclim, Maxent, and Support Vector Machine algorithms, evidenced stable areas of strong environmental suitability in the east of the Chapada Diamantina. The models also show an expansion of areas with environmental suitability during the Mid-Holocene, with retraction in the present and greater reductions predicted in future global warming scenarios. The number of individuals in the plots varied from zero to 14, indicating an aggregated distribution. Morisita's index indicated a random distribution along a forest edge but aggregated in the forest interior. *Eschweilera tetrapetala* is sensitive to climatic change and anthropogenic pressure, at both regional and local scales.

Key words: climatic suitably, forest edge effects, IPCC, Mid-Holocene, spatial clustering.

Resumo
Eschweilera tetrapetala é uma árvore endêmica das Florestas Sazonais Submontanas (SSF) da Chapada Diamantina, remanescentes de floresta Atlântica, Brasil. Os efeitos das mudanças climáticas no padrão de distribuição espacial dessa espécie foram investigados para identificar áreas prioritárias de conservação. Os padrões de distribuição e as densidades populacionais foram obtidos por amostragem de indivíduos em dez transectos de 200 x 10 m e trinta parcelas adicionais de 10 x 10 m situadas em borda e interior de uma área da SSF. Esses dados de ocorrência foram submetidos à Modelagem de Nicho Ecológico usando os algoritmos Bioclim, Maxent e Support Vector Machine. O modelo previsto para sua distribuição atual, usando os algoritmos Bioclim, Maxent e Support Vector Machine (SVM), evidenciou áreas de forte adequabilidade ambiental a leste da Serra do Sincorá. Os modelos determinaram expansão da área de adequabilidade ambiental durante o Holoceno Médio, retração no presente e maiores reduções previstas em cenários futuros. O número de indivíduos nas parcelas variou de zero a 14, indicando distribuição agregada. O índice de Morisita indicou distribuição aleatória ao longo da borda da floresta, mas agregada no interior da floresta. *Eschweilera tetrapetala* é sensível às mudanças climáticas e pressão antropogênica, em escalas regional e local.

Palavras-chave: adequabilidade climática, efeitos de borda linear, IPCC, Holoceno Médio, padrões espaciais.

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Introduction

Eschweilera tetrapetala Mori is an arboreal species endemic to the Atlantic Forest sensu lato that occurs in disjunct interior humid sites occupied by submontane seasonal forests (SSF) within the semiarid Caatinga Domain in the Chapada Diamantina and Serra da Jibóia mountains. It is considered "Endangered" (EN) of extinction and is negatively impacted by deforestation and urbanization (CNCFlora 2012). *Eschweilera tetrapetala* is emblematic of the SSF found along the eastern edge of the Serra do Sincorá Range that have been devastated by advancing human occupation since the early 19th century - although now partially protected by the Chapada Diamantina National Park (CDNP) (Funch *et al.* 2008, 2009; Couto *et al.* 2011; Couto-Santos *et al.* 2015). The plant is locally known as "sapucaia", and its fruits are used for artisanal purposes and its seeds are considered edible (Funch *et al.* 2004; Mori 1995). Recent studies in SSF demonstrated the negative influences of edge effects on *E. tetrapetala* abundance and its floral visitors, and the influence of El Niño and edge effects on its reproductive phenology (Couto-Santos *et al.* 2015; Menezes *et al.* 2018).

The Fifth Report of the Intergovernmental Panel on Climate Change (IPCC) presented evidence of global warming, characterized by changes in rainfall regimes and elevations of atmospheric temperatures of up to 4.8 °C by 2,100 (IPCC 2013). Those climatic alterations will have significant impacts on biodiversity, and even the most conservative predictions suggest that approximately 10% of all species, in all regions of our planet, will become extinct by 2,100 (Maclean & Wilson 2011).

Climatic oscillations have affected species throughout their evolutive histories (Root *et al.* 2003), and studies employing paleoclimatic approaches defend the view that historical geological and climatic processes have acted as modulators of diversity patterns in tropical forests (*e.g.*, Haffer 2008; Vanzolini & Williams 1970). One of the principal hypotheses of those studies is the existence of forest refuges (Haffer 1969; Vanzolini & Williams 1970; Brown & Ab'Sáber 1979), where humid forests retreat during the ice ages, leaving some of humid forest patches as refuges within a matrix of other drier vegetation types. Those forests expanded again during interglacial periods when the climate became more humid. Each time the population was exposed to climatic change, the chances of fragmentation increased, and therefore the possibility of isolation and speciation (Haffer 2008). When subjected to selective climatic pressures, species tend to migrate spatially or evolve into new niches (Martinez-Mayer *et al.* 2004). The velocities of the climate changes predicted for the present century, however, will probably be greater than the adaptive capacities of many species and could result in mass extinctions (Root *et al.* 2003).

Montane and submontane humid refuges inside the semiarid Caatinga are known as "*Brejos de Altitude*", and they harbor humid forests in the midst of the more open and dry forests of the Caatinga domain (Andrade *et al.* 2009; Ledo & Colli 2017). Those climatic differences in the "*Brejos de Altitude*" in relation to lowland Caatinga areas provide a scenario of different levels of genetic diversity that have been studied in attempts to understand the historic patterns that modulate biodiversity in South American tropical forests (*e.g.*, Andrade *et al.* 2007; Andrade *et al.* 2009; Ledo & Colli 2017). As such, better understanding the historic patterns that are modulated the vegetation of the "*Brejos de Altitude*" could provide important information about the processes of previous connection of now isolated humid forest within Caatinga and the Atlantic forest taxa, and how the expansion and retraction of those tropical forests opened and closed migration routes and allowed exchanges between lineages, with posterior diversification.

Ecological niche models (ENMs) can serve as important tools for understanding how environmental factors influence diversity and the distribution patterns of different species, and viewing the paleoclimate as a modulating agent of diversity in the neotropical region can aid in identifying possible refuges and diversity "hotspots" (Carnaval & Moritz 2008; Carnaval *et al.* 2009). ENMs also allow inferences concerning how future climate changes will affect species' niches (Colombo & Joly 2010; Siqueira & Peterson 2003) and aid in determining priority areas for conservation (Ortega-Huerta & Peterson 2004; Silva 2016). To generate those species distribution models, records of species' occurrences are combined with digital overlays of environmental variables to project scenarios that represent their required environmental conditions and/or indicate potential areas of occurrence (Pearson *et al.* 2007).

Another tool that generates important data for understanding the patterns influencing neotropical diversity (and, consequently, biodiversity conservation) is the analysis of the spatial distribution patterns of individuals in plant communities (Anjos *et al.* 2004), as those spatial patterns reflect how species niche requirements interact with spatial and temporal climatic variations (Poulos & Camp 2010). Colombo & Joly (2010) examined the future distributions of 38 arboreal species native to the Atlantic Forest and estimated that there would be future reductions of from 25% to 50% in their areas of potential occurrence. That scenario is quite alarming, because the Atlantic Forest is recognized as one of the 35 global biodiversity hotspots and the fifth richest domain in terms of endemism (Myers *et al.* 2000; Mittermeier *et al.* 2004; Cunha *et al.*2013).

The combination of ENMs with Spatial Distribution Patterns can furnish information important to our understanding of the environmental niche requirements and ecological patterns critical to the long-term preservation of *E. tetrapetala*. As such, we sought to respond to the following questions: i) what is the potential spatial distribution of *E. tetrapetala* in the Chapada Diamantina? ii) Where are the areas of potential environmental suitability for the occurrence of *E. tetrapetala* in the Jequiriça/Paraguaçu Basin in Brazil? iii) How did climatic conditions during the mid-Holocene influence the current distribution pattern of *E. tetrapetalla*?; and, iv) What will be the effects of climate change on its future distribution?

We also sought to test the following hypotheses: i) that the areas of climatic suitability of *E. tetrapetala* will be found in SSF sites along the eastern slopes of the Sincorá Range in the Chapada Diamantina and Serra da Jibóia, in Northeastern Brazil; ii) the areas of climatic suitability for *E. tetrapetala* in the mid-Holocene expanded in that warmer and more humid climate, with posterior retraction under the current, drier climatic conditions in the Caatinga Domain (Buso Júnior *et al.* 2013; Clapperton 1993); iii) in future scenarios, *E. tetrapetala* will suffer losses of areas of environmental suitability due to increasing temperatures and reductions in rainfall rates (IPCC 2013; Torres & Marengo 2013); iv) *E. tetrapetala* should demonstrate an aggregated distribution pattern as it produces zoochoric seeds (Janzen 1970; Gielh *et al.* 2007) and the animals that consume them generally deposit those diaspores in their burrows or along regularly used trails (Schupp *et al.* 2002).

Materials and Methods

Study area and focal species

The study area we used to calibrate the niche model comprised the Paraguaçu River Basin in Brazil - an area that includes the entire known extension of occurrence of *Eschweilera tetrapetala*, which is thought to be endemic to the Chapada Diamantina range and nearby highlands. The Paraguaçu River Basin covers approximately 75,000 km^2, including the Jiquiriça River and Paraguaçu River sub-basins (Vieira *et al.* 2011), and a humid to sub-humid climate, with mean monthly temperatures varying between 16º and 28 ºC; mean annual rainfall rates vary from 500 to 1,200 mm (Vieira *et al.* 2011).

Eschweilera tetrapetala (Lecythidaceae) is a tree restricted to Atlantic Forest remnants relatively distant from the coast in the Chapada Diamantina Mountains in Northeastern Brazil (Funch *et al.* 2008), specifically to the seasonal submontane forests (SSF) situated along the eastern flank of the Serra do Sincorá Range and partially included within the Chapada Diamantina National Park (CDNP) (Fig. 1). A single collection of *E. tetrapetala* was made more than 20 years ago (R.M.H, 28490, HUEFS, in 1997) in another Atlantic Forest site in Serra da Jibóia in the interior of Bahia state. That population, however, may well be extinct, as more recent expeditions to the same area and bibliographic and herbarium searches have not revealed any new records of the species for that locality (Sobrinho & Queiroz 2005; Neves 2005; Costa & Guedes 2010).

Eschweilera tetrapetala is a canopy tree 5–20 m tall and a component of SSF encountered at altitudes between 400 and 800 m a.s.l. on slightly undulating landscapes with clayey red-yellow latosols containing little organic material (Funch *et al.* 2005). The regional climate (type Aw, following Alvares *et al.* 2014) has mean monthly temperatures oscillating around 18 ºC in the Austral winter (April - September), and up to 22 ºC in the warmest months of the year (October - February).

Data collection

Spatial distribution

We estimated the spatial distribution pattern, density, and abundance of *E. tetrapetala* in patches of Atlantic Forest in the Chapada Diamantina by delimiting 10 random 200 × 10 m plots within a forest area along the eastern flank of the Serra

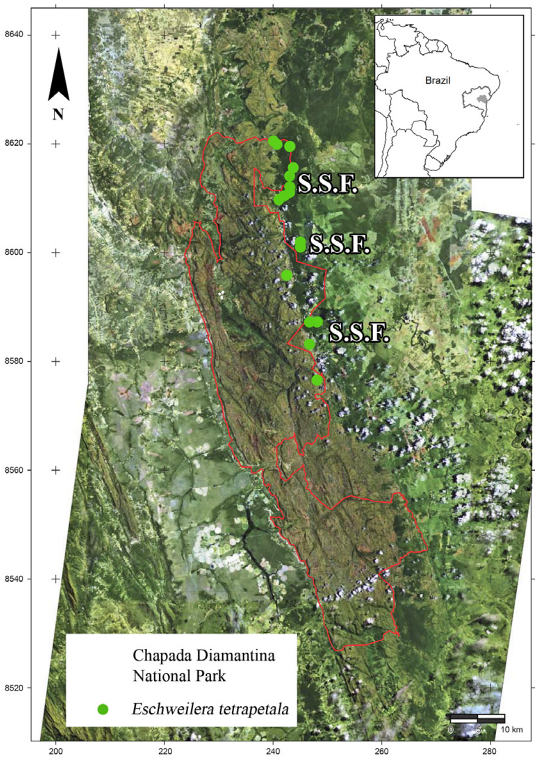

Figure 1 – Location of the Chapada Diamantina National Park (CDNP) and its surroundings, Bahia, Brazil (adapted from Funch *et al.* 2009); on the eastern edge of the CDNP there is the submontane seasonal forest (SSF) where *Eschweilera tetrapetala* Mori (Lecythidaceae) occurs, the target species of this study.

do Sincorá Range. All individuals with DBH $\geq$ 5 cm (1.30 m) were marked. We also used previous data from 30 permanent 10 × 10 m plots (0.3 ha) that were randomly established by Couto-Santos *et al.* (2015) in an area of SSF (12º28'31"S; 41º23'14"W) within the CDNP. The study by Couto-Santos *et al.* (2015) inventoried individuals of *E. tetrapetala* (DBH $\geq$ 5 cm) in 15 plots situated along a forest edge and 15 plots in the forest interior.

The Mann-Whitney (U) test was used to evaluate whether there were variations in the abundances of *E. tetrapetala* individuals within the context of the forest edges and interiors. This non-parametric test represents an alternative to the Student t test, and is used when for comparing two independent samples that belong, or not, to the same population and whose requisites for the application of the Student t test were not fulfilled (Zar 1999). The Mann-Whitney (U) test was performed using open access R software (R Development Core Team 2018).

We analyzed the distribution pattern of the *E. tetrapetala* population using the Standardized Morisita dispersal index (I_p), as it is independent of population density and sample size. The Traditional Morista dispersal index must first be used to calculate Ip ($Id = N(\Sigma x^2 - \Sigma x) / [(\Sigma x)^2 - \Sigma x]$, where N = total number of plots sampled and x = number of individuals). The significance of the data was determined using the chi-squared test (X^2) at a 0.05 level of probability. The Uniformity Index (Mu) Aggregation Index (Mc) were also calculated. The value of the Standardized Morisita Index, which varies from -1.0 to + 1.0, was then obtained using the values of Id, Mu, and Mc. As such, when the standardized I_p value is greater than or equal to 0.5, the spatial distribution of the population is considered aggregated; if that value was less than -0.5, the spatial distribution is considered uniform; if the I_p value is between those two, the species distribution is considered random (Krebs 1999). The above cited analyses were performed using R program software (R Development Core Team 2018), with the vegan package (Oksanen *et al.* 2012).

Preliminary assessment based on extension of occurrence

The Extension of Occurrence (EOO) represents the minimum continuous area that can be defined that includes all of the known, inferred, or projected occurrences of a given taxon, being one of the parameters most frequently utilized by the International Union for Conservation of Nature - IUCN (IUCN 2001) to categorize the degree of threat and/or conservation status of a species (IUCN 2013). We delimited the EOO of *E. tetrapetala* using the same records of occurrence used in the niche modeling. That delimitation used the minimum convex polygon method, which defines the smallest polygon that contains all of the recorded occurrences with no internal angle greater than 180º (IUCN 2001). Those calculations were performed using R program software (R Development Core Team 2018), with the dismo package (Hijmans *et al.* 2017). The conservation status category of the species was evaluated using the criteria proposed by IUCN (2014) based on its area of occurrence.

The Area of Occupation (AOO) is defined by the area within the EOO that is effectively occupied by a given taxon (IUCN 2013). The calculations of the Area Occupation used 2 km grids, as recommended by the IUCN (2013); those calculations were performed using the GeoCAT tool (<http://geocat.kew.org/editor>).

Occurrence records

We obtained the occurrence records of *E. tetrapetala* by consulting the *Species link* (<http://www.splink.org.br/>) and the Global Biodiversity Information Facility (<https://www.gbif.org/>) databanks, through field excursions, and from data from previous studies of that species. Those records were carefully evaluated in terms of their accuracies, and those records considered imprecise (not identified by specialists of the family), duplicates (*i.e.*, collections separated by less than 1 km), and within urbanized areas (as visualized using Google Earth), were not considered. The occurrence data of the species were selected by consulting Michel Ribeiro and Scoot Mori, specialists of the genus *Eschweilera* and the family Lecythidaceae respectively. There are records of the occurrence for municipalities of São Miguel das Matas, Porto Seguro, and Wenceslau Guimarães in databanks (Gbif and Species Link), that are not *E. tetrapetala*, as the above cited specialists indicated that those records are of other species of the genus (*E. mattos-silvae* and *E. complanata*). We thank Michel Robeiro and Scoot Mori for the taxonomic information they provided, which was extremely important for the success of the present study. The records of occurrence for Teresina, in Piauí state, likewise not referred to *E. tetrapetala*.

Climatic variables

We selected five predictive variables to be used among the 19 bioclimatic variables (resolution 30 seconds of arc [~1 km]) available on the WorldClim site (<https://www.worldclim.org/data/index.html>) (Hijmans *et al.* 2005). All the variables were cropped to a buffer of 50 km surrounding the Jequiriça/Paraguaçu basins. To eliminate redundant variables and minimize the effects of multicollinearity (Peterson *et al.* 2011) we selected bioclimatic layers from among all of the 19 available variables using correlation analysis (Spearman coefficient), eliminating layers if they produced correlation values greater than 0.60 ($r < 0.60$) (Warren *et al.* 2014). The bioclimatic layers selected were temperature seasonality (Bio4), maximum temperature of three warmest months (Bio5), minimum temperature of the three coldest months (Bio6), rainfall seasonality (Bio15), and rainfall in the warmest trimester (Bio18)(see supplementary material: <https://doi.org/10.6084/m9.figshare.12524081.v1>)

To statistically describe the environmental factors that most influenced the occurrence of *E. tetrapetala*, we extracted their values from the occurrence records using ArcMap v. 10 (ESRI, Redland, CA) and then calculated their means and standard errors.

Projections

The historic distribution of *E. tetrapetala* was projected using all of the models available on the WorldClim site (Tab. 1) and the same bioclimatic variables used for projecting its current potential distribution but considering paleoclimatic data obtained from climatic simulation models (Tab. 1).

To model the future distribution of *E. tetrapetala* (with predictions for 2070), we considered the following general circulation models (GCMs): CCSM4, MIROC-ESM, HadGEM2-ES (Tab. 1). Those models were evaluated by IPCC (2013) in the fifth evaluation report (AR5), and present the results for future scenarios with different concentrations of greenhouse gases, pollution emissions, land-use alterations, and the adaptive capacities and vulnerabilities of socio-economic systems. For future scenarios we adopted two categories within the Representative Concentration Pathways (RCP): RCP 4.5 and RCP 8.5. The RCP 4.5 categories are considered the most realistic optimist scenarios, with predicted temperature increases of between 1.1 °C and 2.6 °C. The RCP 8.5 categories are considered more pessimistic, predicting greater increases in hothouse gases along the 21st century, with temperature elevations reaching 4.8 °C (IPCC 2013).

We used the same variables of the "present" models (listed in Tab. 1) as predictors to project the niche models of both historic (mid-Holocene, ~6,000 years BP) and future (projections for 2070) scenarios.

Modeling

We used the Bioclim, Maxent, and Support Vector Machine (SVM) algorithms to instruct the ecological niche models of *E. tetrapetala*. Model validations were performed using crossed validation (k-fold) (Fielding & Bell 1997; Pearson *et al.* 2007), dividing the data randomly and utilizing 75% of the occurrence records to train the model and 25% to test it. That procedure was repeated five times, totaling 20 models per algorithm. Model

Table 1 – Global climate models (GCMs) using niche modeling of *Eschweilera tetrapetala* Mori in past (mid Holocene ~ 6,000 years) and future scenarios (predictions for 2070). The X indicates the Global climate models (GCMs) that were used in each scenario (past, present and future) to elaborate the final model.

Global Climate Models (GCMs)	Mid-Holocene (~ 6.000 years)	Future (2060–2080)
BCC-CSM1-1	X	-
CCSM4	X	X
CNRM-CM5-	X	-
HadGEM2-CC	X	-
HadGEM2-ES	X	X
IPSL-CM5A-LR	X	-
MIROC-ESM	X	X
MPI-ESM-P	X	-
MRI-CGCM3	X	-

performances were then statistically evaluated using the area under curve method (AUC) and True Skill Statistic (TSS) (Allouche *et al.* 2006; Phillips & Dudik 2008). A final model (including the different GCMs) was then developed based on the median of all models with TSS values > 0.7.

The TSS calculation was performed using the Maximum training sensitivity plus specificity logistic threshold to transform the logistic output into a binary one (suitable conditions versus unsuitable conditions).

Priority areas for conservation

We used a multi-model approach employing the means of the layers, which can diminish uncertainties related to the projections and present the climate in any given historical period in a more robust manner. As such, we opted for a consensus model (ensemble) in each period evaluated (past and future) using the means of all the models (Harris *et al.* 2014). The final consensus models for each period evaluated (past and future) were converted into binary models using the Maximum training sensitivity plus the specificity logistic threshold, as the present study was designed to identify potential areas for *E. tetrapetala* conservation (Liu *et al.* 2005) with potential climatic stability (adapted from Silva 2016).

To identify potential areas of climatic stability, we summed the respective historical models and the current distribution of *E. tetrapetala* and then calculated the numbers of suitable pixels in the respective models. That allowed us to evaluate the environmentally suitable areas that were lost, as well as those that remained suitable in both past and present scenario. The consensus areas resulting from the sum of those models were considered potential areas of climatic stability for the focal species.

To identify priority areas conservation, we proceeded in a similar manner to the methodology used to define potential areas of climatic stability, although summing the distribution models for the current period with future models in the RCP 4.5 and RPC 8.5 scenarios. We then calculated the numbers of pixels and the areas of environmental suitability that were lost and those that remained suitable in both present and future scenarios. The consensus areas resulting from the sum of those models were identified as priority areas for *E. tetrapetala* conservation. (see supplementary material <https://doi.org/10.6084/m9.figshare.12524081.v1>).

Results

Spatial distribution and preliminary assessment based on extension of occurrence

We encountered 55 individuals of *E. tetrapetala* (183 individuals/ha) in the sampled permanent plots, of which only six individuals occurred along the forest edge; plus 36 additional individuals encountered in the plots along the eastern flank of the Serra do Sincorá (7 individuals/ha). Significant differences were observed in terms of the abundances of individuals in the forest edge and interior (U = 49, p = 0.005), with abundance being six times greater in the forest interior than along its edge, considering all individuals.

The numbers of individuals inside the plots varied from zero to 14 in the two sampling areas, indicating aggregated spatial distributions in both the permanent plots (e $I_d = 3$, $M_c = 1.30$ and $M_c = 0.76$, and $I_p = 0.52$) and the eastern flank plots ($I_d = 2.68$, $M_c = 0.82$ and $M_u = 1.29$, and $I_p = 0.58$). Morisita's standardized index (I_p) calculated for the permanent interior plots ($I_d = 1.94$, $M_c = 1.25$ and $M_u = 0.82$, and $I_p = 0.52$) and for the permanent forest edge plots ($I_d = 1.42$, $M_c = 3.21$ and $M_u = -0.39$, and $I_p = 0.10$) revealed a clumped grouping pattern in the interior but a possible random pattern along the forest edge.

The preliminary assessment of the EOO of *Eschweilera tetrapetala* in the Serra do Sincorá Range is 4,791 km² (EN), comprising forest formations along the eastern flank of that range (Fig. 2). The calculated AOO was 60 km² (EN).

Predictive models of current distributions

The extractions of values of the bioclimatic layers with records of the occurrence of *E. tetrapetala* point to climatic and topographic characteristics typical of submontane seasonal forests - as the areas of greatest probability of occurrence of *E. tetrapetala* are situated in localities with annual precipitation rates between 1,000 and 1,500 mm, mean annual temperatures between 22 and 24 °C, and altitudes between 350 and 600 m a.s.l. (Oliveira-Filho & Fontes 2000; Funch *et al.* 2008, 2009; Alvares *et al.* 2014; ICMBIO 2007).

The ENMs generated for *E. tetrapetala* in all the scenarios tested demonstrated sound statistical results, with a mean TSS of 0.90 ± 0.1 (standard error) and a mean AUC of 0.94 ± 0.06. The predictive model for the current distribution of *E. tetrapetala* indicated climatic environmental suitability within the only 294 km² of that area

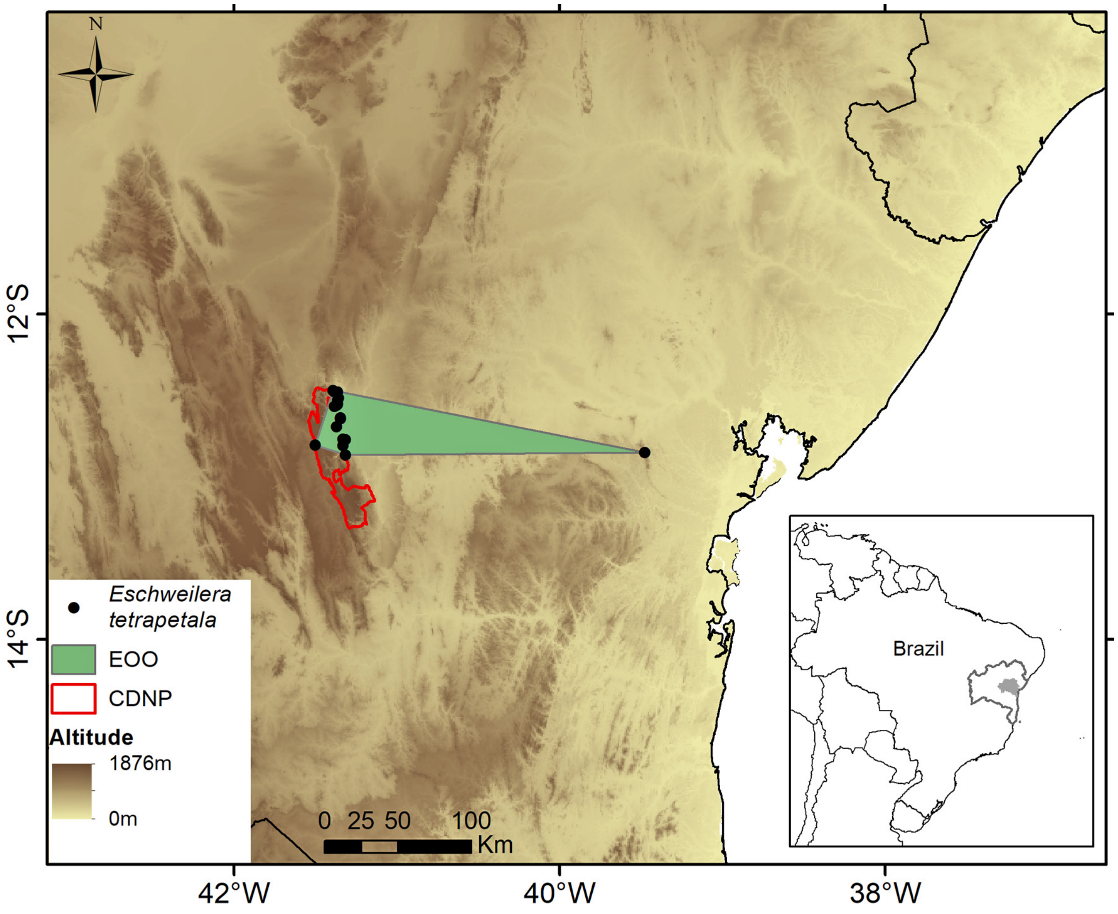

Figure 2 – Map of the Occurrence Extension (EOO) of *Eschweilera tetrapetala* Mori in the Sincorá Range, highlighting the boundaries of the Chapada Diamantina National Park, Northeastern Brazil.

still retains remnant Atlantic Forest sites. High climatic environmental suitability values, however, were principally concentrated in the SSF occurring along the eastern border of the CDNP in the Serra do Sincorá Range (Fig. 3a).

Predictive models of past distributions

Paleoclimatic reconstructions for the mid-Holocene (~6,000 years BP) indicated an expansion of *E. tetrapetala* distribution (Fig. 3b), followed by retraction in modern times (Fig. 3a).

Predictive models of future distributions

The projections for future scenarios (2070) indicated a perceptible reduction in the area of climatic environmental suitability, evidencing a future shrinkage in the distribution of *E. tetrapetala* in the Chapada Diamantina (Fig. 4). The RCP 4.5 scenario (the most optimistic) indicated areas of climatic environmental suitability for the species comprising 81,724 km^2. In RCP 8.5 (the most pessimistic) scenario the areas of climatic environmental suitability would extend over

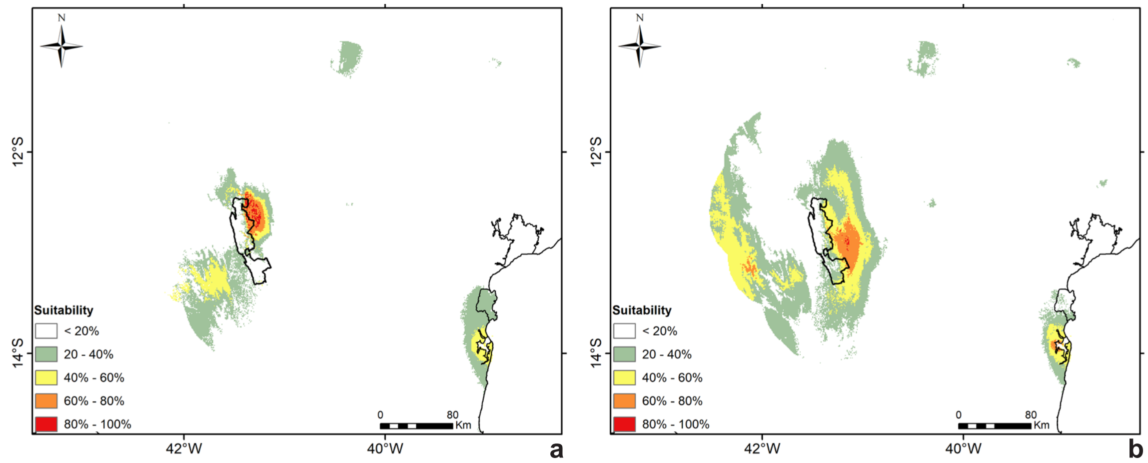

Figure 3 – a. Predictive model of current environmental suitability of *Eschweilera tetrapetala* Mori in the Sincorá Range, emphasizing the boundaries of the Chapada Diamantina National Park, Northeastern Brazil. b. Paleoclimatic reconstruction for the Holocene Middle from the projections of current potential distribution models of *Eschweilera tetrapetala* Mori.

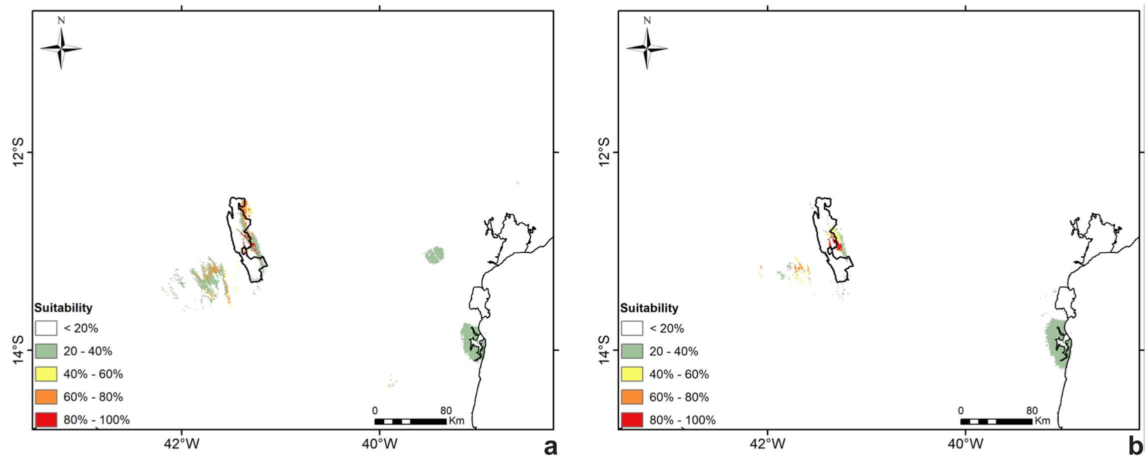

Figure 4 – a-b. Projections for the year 2070 – a. optimistic scenario (RCP 4.5), on the left; b. pessimistic scenario (RCP 8.5), on the right. These models were projected from current potential distribution models of *Eschweilera tetrapetala* Mori.

54,192 km^2 in the Chapada Diamantina, including SSF that occur along the eastern border of the CDNP and neighboring regions of the Serra do Sincorá Range.

Potential areas of climatic stability and priority areas for *E. tetrapetala* conservation

The current distribution of *E. tetrapetala* represents a retraction of approximately ~48% as compared to the area of climatic environmental suitability in the mid-Holocene. The glacial refuges projected by the models for past and present distribution extensions include a small portion of the SSF near the CDNP in the Serra do Sincorá Range, and another portion along the southern Atlantic coast of Bahia state (Fig. 5). According to the models projected for the future, *E. tetrapetala* will reduce to 41% of its area of environmental suitability as compared to its current predictive distribution under the most optimistic realistic scenario (RCP 4.5), and to 24% in the most pessimistic scenario (RCP 8.5). The priority areas for *E. tetrapetala* conservation, according to the models generated for the current and future scenarios (11,265 km^2), comprise a remnant portion of Atlantic Forest in the Serra do Sincorá and expand through neighboring areas - as well as a section of eastern Bahia state (Fig. 5). Of that total area, only 4.5% will be protected within the CDNP (502 km^2).

Discussion

Our results confirmed the original hypotheses of this study, as the predictive model for the current distribution of *E. tetrapetala* includes areas of strong environmental suitability in remnant inland areas of Atlantic Forest within the Caatinga Domain, in submontane seasonal forests. Those forests grow on yellow latosols on the eastern flank of the Serra do Sincorá Range of the Chapada Diamantina (Funch *et al.* 2008).

That potential distribution coincides with the true known distribution of the species (Funch *et al.* 2005, 2008; Couto-Santos *et al*. 2015). *Eschweilera tetrapetala* is the only arboreal species restricted to the SSF along the eastern flank of the Serra do Sincorá Range and is considered an indicator endemic species of that forest (Funch *et al.* 2005, 2008).

The model generated for the current potential distribution of *E. tetrapetala* does not predict Serra da Jibóia as an area of climatic suitability. That result could be due to the fact that: i) the current population represents a remnant group with an historically more ample distribution that may now be in decline; ii) the species can occur in areas such as Serra da Jibóia, but as it only appeared as a single point of occurrence, the model did not give it much weight and did not consider it a relevant area; iii) that point may reflect only one (or a few) individual(s) that were "in transit", and were, for some reason, established there, but not

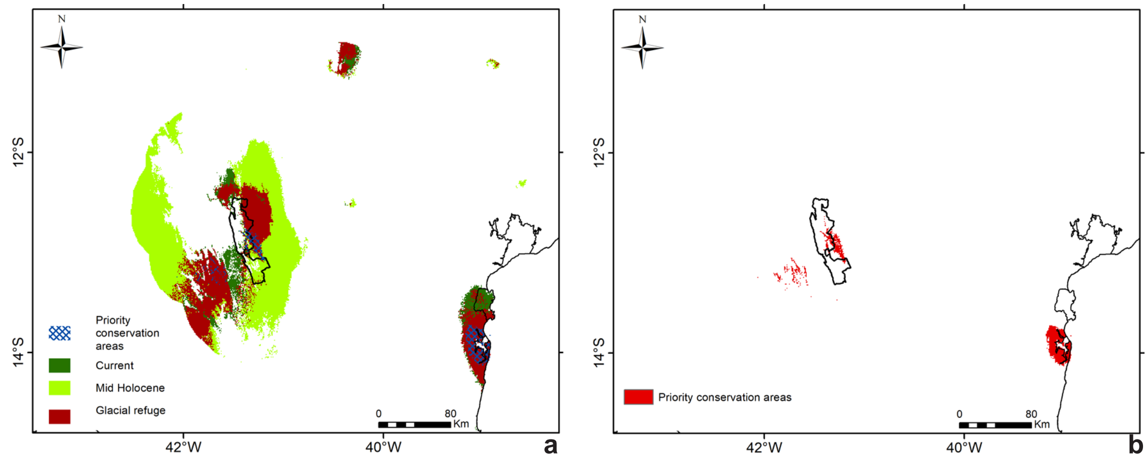

Figure 5 – a. Consensus map indicating stable areas for *Eschweilera tetrapetala* Mori during current climate niche projections and paleoclimatic reconstructions of the Mid-Holocene. Cross hatchings indicate priority areas for conservation. b. Indications of priority areas for the conservation of *Eschweilera tetrapetala* Mori.

in a definitive sense (perhaps not leaving viable descendants and therefore not creating a self-sustaining population); iv) the species may, in fact, occur in areas with environmental conditions similar to Serra da Jibóia, but there is no additional information available about them; v) its omission could represent a true error in the model, as all models are approximations of reality and always have some associated errors to certain degrees. The least probable option, however, is “v”, as we undertook strenuous adjustments of the model to minimize such errors. Smith *et al.* (2016) noted that there were very few populations of *E. tetrapetala* relatively distant from the town of Lençóis, and that there was only a single collection of that species from Serra da Jibóia, Bahia, made more than 20 years ago (in 1997 by R. M.H, 28490, HUEFS). As such, we suggest that the population at Serra da Jiboia is in decline or possibly even extinct.

The paleoclimatic reconstructions projected for *E. tetrapetala* are distinct from those suggested for species occupying the high lands of southwestern Brazil and the montane refuges of Caatinga areas by Ledo & Colli (2017). *E. tetrapetala* demonstrated a behavior more similar to lowland taxa (called “warmer group”) that expanded their range during the interglacial periods. Within that context, is worth pointing out that the hypothesis that defends the idea that Lecythidaceae species could have gradually migrated along the highest and most human areas (called “brejos”) from the Amazon to the Atlantic Forest appears improbable, as most species of Lecythidaceae cannot form seeds by self-pollination, and it is difficult to imagine that two trees of the same species dispersed seeds from one “brejo” to another to be able to realize cross-pollination (Moritz 1984, Mori *et al*. 2016).

A predominantly humid climatic phase occurred in the late Holocene (between ~7000-4000 BP) that could have favored expansion of humid tropical forests in areas currently occupied by the deciduous caatinga (Buso Júnior *et al.* 2013). The return of a warmer and more humid climate after the dryer periods of the last Glacial Maximum was evidenced by the pollen analyses of Garcia *et al.* (2004) in an area of seasonal forest in the Paraíba River Valley in São Paulo state. That area has climatic and topographic conditions similar to that of the SSF area along the eastern flank of the Serra do Sincorá Range. From approximately 3500 BP to the present, the climate returned to cooler and drier conditions, establishing the current seasonal climate (Garcia *et al.* 2004; Buso Júnior *et al.* 2013), which probably resulted in reductions of forest cover.

Future scenarios predict a perceptible retraction of areas of climatic environmental suitability, reinforcing the importance of the CDNP for the maintenance of *E. tetrapetala* in an era of climate change. The predicted reductions of areas of environmental suitability for *E. tetrapetala* reflect expected temperature increases and rainfall reductions in Northeastern Brazil (Marengo *et al*. 2011). Similar reductions in the areas of environmental suitability for Atlantic Forest species were reported by Colombo & Joly (2010), who modeled the potential distributions of 38 arboreal species of that biome and evidenced a 28% reduction in potential areas of occurrence under the most optimistic climate change scenario, and potential reductions in areas of 25% to up to 50% in the most pessimistic scenario.

As there are no predictions that tropical forests will expand as they did in the Holocene, accelerated processes of both climate change and Atlantic Forest fragmentation (Colombo & Joly 2010) essentially make natural processes of expansion and retraction of *E. tetrapetala* unviable, as we observed in the present study for the mid-Holocene. Research indicates that until 2070, even the most stable Neotropical forests will suffer altered conditions, with drastic reductions resulting in savanization (Anadon *et al.* 2014).

The SSF along the eastern border of the CDNP (and neighboring areas) are likewise included in that scenario. According to Funch *et al.* (2005), that region represents the largest contiguous forested area in the Chapada Diamantina Mountains – although it is increasingly experiencing deforestation and clearing, which increases the vulnerability of *E. tetrapetala*. As such, the ENMs generated in the present study to indicate priority areas for the conservation of *E. tetrapetala* are of extreme importance for conservation and management plans, as they indicate potential preservation areas with climatic conditions suitable for that species to persist over long periods of time, even when faced with adverse climatic conditions and anthropic threats.

The use of ENMs to identify habitats suitable for the conservation of focal species over wide geographic scales becomes most useful when associated with their ecological characteristics, as for example, information concerning population dynamics (Heinrichs *et al.* 2010). Hay *et al.* (2000) noted that the elucidation of the spatial distribution pattern of a given species represents one of the first steps in understanding its population dynamics, as it reflects spatial heterogeneity and the influences of abiotic and biotic factors – which indicate the level of adaptability of that plant to selective pressures (Lima-Ribeiro 2008).

When faced with climate change, species can either migrate or modify their niche requirements (and possibly escape extinction). When a species does not have the capacity to colonize new areas that would allow it to compensate for extreme external environmental conditions, it will necessarily have its area of occurrence reduced, and possibly face extinction (Martinez-Mayer *et al.* 2004). This seems to be the case of *E. tetrapetala,* as the species of the family Lecythidaceae disperse their seeds through zoochory (the principal dispersal agents being rodents) or by barochory (Mori *et al.* 1981), without a high probability of their propagules traveling long distances. When the fruits mature and open, their seeds are dispersed by rodents (or simply fall to the ground) (Mori *et al.* 1981). That type of dispersal favors seed accumulation near the mother plant, where they are more susceptible to predation or pathogens, as well as secondary dispersal (Vilela *et al.* 2012).

The aggregated spatial distribution observed with *E. tetrapetala* has been reported for other species of the genus, such as *E. coriacea* (DC.) Mori. (Lopes 2007) and *E. pedicellata* (Rich.) Mori (Souza *et al.* 2014), as well as other genera of Lecythidaceae, such as *Bertholletia excelsa* Bonpl. and *Lecythis lúrida* (Miers.) S.A. Mori. (Carvalho 1992). Their observed aggregated distribution patterns reflect their specific dispersal mechanisms (Janzen 1976), the establishment of young individuals only in the specialized habitat required by the Lecythidaceae (Mori *et al.* 1978). Couto *et al.* (2015) demonstrated the predominance of *E. tetrapetala* in SSF in the Serra do Sincorá Range, and its high Importance Value (42.3%) and high Relative Density (22.5%) in the forest interior - in contrast to its low Importance Value (6.53%) and low Relative Density (2.49%) along the forest edge. That edge effect strongly emphasized its susceptibility to alterations resulting from habitat fragmentation, as its aggregated distribution in the forest interior is a consequence of its grouping in more favorable, but more restricted, habitats (Ludwig & Reynolds 1988). Habitat fragmentation not only impacts the abundance and distribution patterns of populations, but also influences growth rates, plant-animal interactions, seed production, and the sizes of individuals (Lima-Ribeiro 2008). Menezes *et al.* (2018) observed that the numbers of floral visitors as well as fruit production by *E. tetrapetala* were reduced along the forest edge as compared to the forest interior.

The distinct distribution patterns and population abundances of *E. tetrapetala* noted along the forest edge and in the interior can aid in selecting sites for long-term conservation efforts, as the probabilities of occurrence furnished by the ENMs are not always correlated with environments fully suitable for the occurrences of a given species at very local scales (*e.g.*, areas of probable occurrence can contemplate pastures or highly fragmented landscapes) (Guisan *et al.* 2013). As such, it will be necessary to combine ENMs with a detailed understanding of the biology of any species, as fragmentation can often seriously reduce long-term persistence. Due to the reduction in the extent of occurrence of *E. tetrapetala*, associated with the declines of continuous stands of Atlantic Forest, as well as deforestation of the SSF along the eastern boundary of the CDNP (Funch *et al.* 2005, 2008) *E. tetrapetala* was categorized as endangered (EN) according to criteria B1ab (iii) + 2ab (iii) of IUCN (2013). We reinforce here its status of threatened with extinction, as suggested by Smith *et al.* (2016), because its survival will be seriously impacted by the reduction of its ecological niche due to climate change as well as anthropogenic impacts at both regional and local scales. Strategies for the conservation of *E. tetrapetala* should be included in the National Action Plan for the conservation of species threatened with extinction, as well as for conservation measures directed at the SSF - which is only partially protected by the CDNP.

Supplementary material

The records of *E. tetrapetala*, values of climatic variables for each site, models of the species under different scenarios in raster format and the R code used in the analyses are available to the reader at <https://doi.org/10.6084/m9.figshare.12524081.v1>.

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