








Climate change will likely threaten areas of suitable habitats for the most relevant medicinal plants native to the Caatinga dry forest

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ABSTRACT

Disruption of ecosystem services associated with climate change may affect human well-being in different ways. Medicinal plants provide extremely relevant ecosystem services. Here, we tested the hypothesis that highly suitable habitats (i.e., suitability ≥ 0.8) for medicinal plants in Caatinga dry forest may be potentially contracted under scenarios of climate change, which are represented by different levels of increases in greenhouse gas emissions. We performed species distribution modelling to simulate the effects of climate change on the range of suitable habitats for medicinal plants native to the Caatinga dry forest. We selected the 10 most important plant species based on their high local importance as medicinal resources. We documented that climate change may distinctly affect areas of suitable habitats for medicinal plants in the Caatinga dry forest. Independent of the future climatic scenario projected to 2090, 70% of the studied species will likely experience reductions in their areas of highly suitable habitats and 30% will likely experience increases. Specifically, suitable habitats will likely be reduced for (1) *Amburana cearensis*, (2) *Anadenanthera colubrina*, (3) *Bauhinia cheilantha*, (4) *Myracrodruon urundeuva*, (5) *Neocalyptocalyx longifolium*, (6) *Operculina hamiltonii*, (7) *O. macrocarpa*; and will likely be increased for (1) *Cereus jamacaru*, (2) *Erythrina velutina*, (3) *Maytenus rigida*. We also documented a reduction in medicinal plant species richness and composition in all three future climatic scenarios analyzed. We alert that potential future contractions of highly suitable habitats for the most important medicinal plants may compromise ecosystem functions and the provisioning of relevant natural medicines, mainly to low-income communities, which are abundant in the Caatinga dry forest.

Keywords: Ecosystem services; Natural medicines; Northeastern Brazil; Seasonally dry tropical forests; Species distribution.

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SIGNIFICANCE STATEMENT

To understand how climate change in the northeastern region of Brazil will likely affect the range and distribution of suitable habitats for the 10 most relevant medicinal plants native to the Caatinga, the most diverse seasonally dry tropical forest on Earth, we applied species distribution modelling for these plant species under three scenarios of projected climate change. We documented that 1) independent of the future climatic scenario, 70% of the medicinal plant species with high local importance in the Caatinga dry forest will likely experience reductions in their areas of highly suitable habitats; 2) annual precipitation and elevation are the most relevant variables to the distribution of medicinal plant species in the Caatinga dry forest; 3) independent of the future climatic scenario, medicinal plant species richness tends to decrease; 4) reductions in suitable habitat for medicinal plants will likely compromise ecosystem functions 5) future reductions in suitable habitat for medicinal plants will likely reduce the possibility of treating diseases by low-income communities in the Caatinga dry forest.

INTRODUCTION

Climate change, which is directly associated with global warming, is affecting all regions of the world, with observed changes in weather and climate extremes. There is already an increase in 1) hot extremes in most inhabited regions, 2) heavy precipitation in several regions, and also an increase in the 3) probability of agricultural and ecological collapse in some regions (IPCC 2021). In this sense, changes in climate alter the dynamics of different levels of biological organization, including individuals (genetic diversity, physiology and morphology), species (range size and location, habitat quality and quantity), populations (recruitment, migration, timing of budding and flowering), communities (biomass, primary productivity, species interactions) and ecosystems (processes and services) (Houghton *et al.* 2001; Malhi and Wright 2004; Malhi *et al.* 2008; Scheffers *et al.* 2016). The effects of these changes, especially those related to species distribution, persistence and diversity, have been widely reported for plants (e.g., Pimm *et al.* 1995; Prado 2000; Peterson *et al.* 2002; Thomas *et al.* 2004; Botkin *et al.* 2007; Loarie *et al.* 2008; Thuiller *et al.* 2008; Silva *et al.* 2019).

Many of these species present medicinal properties that are strongly associated with human well-being (e.g., Augustino and Gillah 2005, Albuquerque *et al.* 2018, Pompermaier *et al.* 2018). Climate change has the potential to contract areas of suitable habitat for aromatic and medicinal plant species across different regions (Khanum *et al.* 2013; Tangjitman *et al.* 2015; Munt *et al.* 2016; Roy and Roy 2016; Zhao *et al.* 2017; Gupta *et al.* 2019). As a consequence of climate change, ecosystem functions and the provision of services, including food production, water storage, supply of natural medicines, local climate regulation and human well-being, may also be affected (Mooney *et al.* 2009; Nelson *et al.* 2013).

Scientists around the world have drawn attention to the effects of climate change on medicinal plants, highlighting several damaging effects that may affect

the future availability of these resources (e.g., Applequist *et al.* 2020). Medicinal plants play an important role in providing ecosystem services, such as local cultural services and those including economic value, and human well-being, especially in poor regions (Klein *et al.* 2008). The use of plants to improve living conditions and to increase the chances of survival comes from the beginning of human life (Balick and Cox 1997). Plants have numerous purposes for humanity, including food, medicine, clothing and housing, and ornamental use (Balick and Cox 1997). Medicinal plants, in turn, are indispensable for maintaining the health and safety of people in different parts of the world. Currently, in many South American countries, approximately 80% of the population uses medicinal plants (Firmo *et al.* 2011), revealing a high degree of dependence (Nunes and Albuquerque, 2018). The number of studies on medicinal plants has increased significantly worldwide since the 1990s (Nunes and Albuquerque 2018). Since climate change may affect species distribution and physiology (e.g., Scheffers *et al.* 2016), it may become an important threat to medicinal plant species and their ecosystem services (Borges *et al.* 2017a; Gupta *et al.* 2019).

Distinct patterns and consequences of climate change have been predicted across different regions of the world (Scheffers *et al.* 2016; Mansfield *et al.* 2020). In the case of tropical regions, high rates of species loss in response to climate change are expected (Sheldon 2019). Species distribution models (SDMs) trained on presence-only occurrence data have been frequently used to assess the effects of climate change on medicinal plants (e.g., Tangjitman *et al.* 2015; Munt *et al.* 2016; Kaky and Gilbert 2017; Zhao *et al.*, 2017; Asase and Peterson 2019). The species distribution model approach based on the maximum entropy theory (e.g., Phillips *et al.* 2006) allows the prediction of where the species is favored based on the environmental characteristics of the landscape, even if the entire landscape has not been sampled densely (e.g., Phillips *et al.* 2006). Although habitat suitability may expand for some

medicinal species (e.g., Li *et al.* 2019), there is a general trend indicating that climate change may contract suitable habitats for medicinal plants across different regions of the world (e.g., Khanum *et al.* 2013; Munt *et al.* 2016; Roy and Roy 2016; Zhao *et al.* 2017), including tropical regions (e.g., Tangjitman *et al.* 2015; Cavalcante *et al.* 2020).

The Brazilian Caatinga is a seasonally dry tropical forest (SDTF) particularly rich in medicinal plant species. In total, 385 medicinal plant species, of which 275 are native, were observed in the Caatinga dry forest (Albuquerque *et al.* 2007). Representing one of the largest and most diverse semiarid regions in the world, the Caatinga dry forest covers 912,529 km² in northeastern Brazil (Silva *et al.* 2017a). It is surrounded by the Atlantic forest domain to the east and the Cerrado to the west and south. Seasonality due to low and irregularly distributed rainfall, associated with elevated temperatures and highly variable edaphic conditions, results in a diverse spectrum of Caatinga dry forest phytogeographic formations (e.g., Sampaio 1995; Cardoso and Queiroz 2007; Moro *et al.* 2014; Moro *et al.* 2015). It is important to mention that the Caatinga dry forest is inhabited by low-income people who use forest resources intensely for their survival (Albuquerque *et al.* 2017). This use of natural resources by human rural populations may exacerbate the effects of climate change of the biodiversity (e.g., Applequist *et al.* 2020).

Future climatic conditions for the Caatinga dry forest indicate that some regions will likely experience high levels of aridity and subsequent desertification (Marengo *et al.* 2017; Silva *et al.* 2019). It is already known that Caatinga dry forest plants have different susceptibilities to climate change (e.g., Silva *et al.* 2019 and references therein). Specifically, habitat suitability for endemic plants may be associated with climate change, where plants with specialized reproductive strategies will tend to lose a higher proportion of suitable habitat than those with generalist strategies (Silva *et al.* 2019). Drastic contractions in suitable habitats were also observed for plant species nonendemic to the Caatinga dry forest, such as the cactus *Epiphyllum phyllanthus* (L.) Haw. (Cavalcante *et al.* 2020). In this scenario, the Caatinga dry forest represents a great opportunity for studies related to the reproductive profile and perspectives of vulnerability of medicinal plant species to climate change, which may serve as a basis for the development of projects of sustainable use and biodiversity conservation.

In this study, we aimed to understand how climate change in the northeastern region of Brazil affects the range and spatial distribution for the 10 most relevant medicinal plants native to the Caatinga dry forest. We tested the hypothesis that the spatial distribu-

tion for these plant species in the Caatinga dry forest may be reduced under scenarios of projected climate change. We expected that increases in greenhouse gas emissions, as predicted by climate models, may be associated with the contraction of spatial distribution for the most relevant medicinal plants in the Caatinga dry forest.

MATERIAL AND METHODS

Selection of medicinal plant species in the Caatinga dry forest

Based on the 275 species of native medicinal plants listed for the Caatinga dry forest (Albuquerque *et al.* 2007), we generated a list of 10 species native to this phytogeographic domain. The medicinal plant species analysed in this study were 1) *Myracrodruon urundeuva* Allemão (Anacardiaceae), 2) *Cereus jamacaru* DC (Cactaceae), 3) *Neocalyptrocalyx longifolium* (Mart) Cornejo & Iltis (Capparaceae), 4) *Maytenus rigida* Mart (Celastraceae), 5) *Operculina hamiltonii* (G Don) DF Austin Staples, 6) *Operculina macrocarpa* (L) Urb (Convolvulaceae), 7) *Amburana cearensis* (Allemao) AC Sm, 8) *Anadenanthera colubrina* (Vell) Brenan, 9) *Bauhinia cheilantha* (Bong) Steud and 10) *Erythrina velutina* Willd (Leguminosae). These 10 species were selected based on their relative importance index (RI), which is a popular measure in ethnobotanical approaches (e.g., Albuquerque *et al.* 2006). This index measures the use importance of medicinal plants based on therapeutic indications (see Bennett and Prance 2000 for details). In the Caatinga dry forest (Figure 1), the RI of medicinal plants ranged from 0.2 to 2.0 (Albuquerque *et al.* 2007). RI values close to two indicate high versatility of a given species in terms of its medicinal properties. The native selected species exhibited *RI*1.5 (Table 1), indicating their widespread use for the treatment of many diseases by human native populations living in areas of Caatinga dry forest (*sensu* Albuquerque *et al.* 2007). The medicinal applications and the parts of the plants that are used are available in Table S1. The reproductive traits of each medicinal plant species are described in Table 1.

Occurrence data

We required georeferenced data (native occurrence) of the 10 most relevant medicinal plant species native to the Caatinga dry forest. Thus, precise occurrence information of the studied species was accessed in 1) The Global Biodiversity Information Facility platform is an international data network funded by governments around the world, providing open access to data on all life on Earth (GBIF

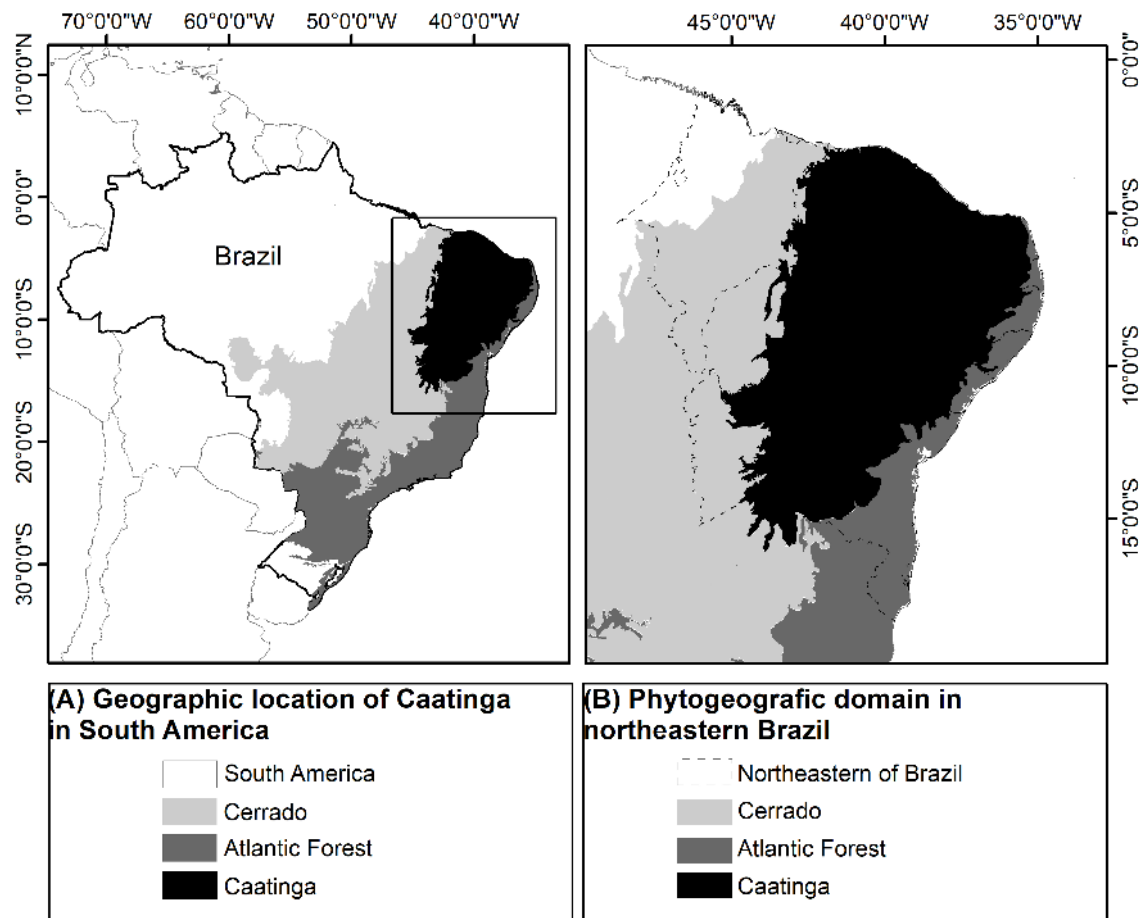


Figure 1. Geographical location of the Caatinga dry forest in South America (A) and phylogeographic domains in northeastern Brazil (B). Source of the shapes: MMA (<http://mapas.mma.gov.br/i3geo/datadownload.htm> and http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm?caatinga/dados/shape_file)

2021) (<https://www.gbif.org>, accessed May 2022); 2) REFLORA - Herbário Virtual, virtual herbarium network that contains information on Brazilian plants that are deposited in 63 herbaria in Brazil and 10 international herbaria (<http://reflora.jbrj.gov.br/reflora/herbarioVirtual>, accessed May 2022); 3) Botanical Information and Ecology Network Platform (BIEN), a global information network that helps to document patterns of plant diversity, trait records and distribution, which includes georeferenced plant observation data from herbarium records, plots, survey inventories (<https://bien.nceas.ucsb.edu/bien/biendata>, accessed May 2022) and 4) 95 botanical monographs and floras (for more information see Table S2 in [Supplementary Data](#)). To access the BIEN database, we use the BIEN package (Maitner *et al.* 2018) available for the R 4.1.1 environment (R Core Team, 2021). We excluded from the analysis all repeated and mismatch occurrence data for each species. We used all the available points for

the studied species. We obtained 11,126 geographical coordinates for the species, covering the whole area of natural occurrence, including the phylogeographical domain of the Caatinga dry forest. Table S3 contains the DOI of each occurrence search by species in GBIF and Table S4 summarizes the georeferenced data of medicinal species after removing duplicates and points outside the Caatinga dry forest limits, therefore allowing replication (e.g., Tahei *et al.* 2021).

Current and future climatic variables

We downloaded climate data (2.5 minutes spatial resolution = ca. 21.4 km²) from WorldClim project 2.1 for the current period (average for the years 1970 - 2000) and the future in 2090 (average 2081 - 2100) (Fick and Hijmans 2017). The WorldClim project included a set of 19 climatic variables that summarize aspects of precipitation and temperature (Fick

and Hijmans 2017). Climate data for the future climate projections between 2081-2100 were based on the Coupled Model Intercomparison Project Phase 6 (CMIP6; Eyring *et al.* 2016). The CMIP6 models available so far tend to have higher climate sensitivity than other previous models (Eyring *et al.* 2016). We selected three Shared Socioeconomic Pathways (SSPs) scenarios, which are based on global population growth, access to education, urbanization, economic growth, resource availability, technology development and demand drivers such as lifestyle changes (Riahi *et al.* 2017). These climate scenarios are inferred from aspects related to the carbon biogeochemical cycle, atmospheric and oceanic chemistry, vegetation types, emission of pollutants, solar radiation, ozone concentration, hydrology and sea ice (IPCC 2021). The three SSPs are (1) SSP2-4.5 (Middle of the Road), represents an optimistic scenario of mitigation and adaptation, where social, economic and technological trends do not significantly change from historical patterns, with moderate population growth, improvement in income inequality and environmental degradation; (2) SSP3-7.0 (Regional Rivalry – A Rock Road), represents a realistic scenario of mitigation and adaptation challenge, with little investment in education, health and technological development in the poorest countries, together with a rapidly growing population and growing inequalities, high environmental degradation, is a pathway for stabilization of radiative forcing by 2100; and (3) SSP5-8.5 (Fossil-fueled Development – Taking the Highway), represents a pessimistic scenario of high challenges for mitigation and low challenges for adaptation, driven by exploitation of abundant fossil fuel resources, this scenario corresponds to the pathway with the highest greenhouse gas emissions and a high increase in terrestrial temperatures (see Riahi *et al.* 2017 and IPCC 2021 for more details). We selected the SSPs scenarios based on the BCC-CSM2-MR (Wu *et al.* 2021), CanESM5 (Swart *et al.* 2019), MIROC6 (Tatebe *et al.* 2019) general circulation models (GCMs), which indicated better performance over arid, semi-arid and neotropical regions (e.g., Silva *et al.* 2019; Cai *et al.* 2020; Fuentes-Castillo *et al.* 2020; Menéndez-Guerrero *et al.* 2020). In addition to these variables, we also used elevation as an edaphic variable from WorldClim project 2.1 (Fick and Hijmans 2017).

To reduce overfitting and collinearity of the 19 climatic variables and elevation, models for each species were performed based on noncorrelated variables in the current and future climate scenarios. Correlations among predictor variables were assessed by principal component analysis (PCA), and we selected as predictor variables the axes responsible for 95% of the total variation of climate variables (De Marco and Nóbrega

2018) within the R 4.1.1 environment (R Core Team, 2021). The predictor variables (1) temperature seasonality (b4), (2) annual precipitation (b12), (3) precipitation of wettest quarter (b16), (4) precipitation of warmest quarter (b18), (5) precipitation of coldest quarter (b19), and (6) elevation were retained in our models. These variables have been considered important for modeling plant species distributions in the Caatinga dry forest (e.g., Marengo *et al.* 2017; Silva *et al.* 2019; Cavalcante *et al.* 2020).

Species distribution modelling

We used three algorithms based on (1) the maximum entropy method (MXD; Fonseca *et al.* 2015; Silva *et al.* 2019), (2) support vector machine (SVM; Drake *et al.* 2006), and (3) random forest (RDF; Sahragard *et al.* 2018) to predict habitat suitability for medicinal plant species native to the Caatinga dry forest. These algorithms are adequate to presence and pseudo-absence data (Andrade *et al.* 2020), as in the localities sampled in this study. For this, we used “ENMTML” package (Andrade *et al.* 2020) within R 4.1.1 environment (R Core Team 2021). A total of 15 replicates were used to calculate each algorithm in each climate scenario (current, SSP 2.45, SSP 3.70, and SSP 5.85) for each medicinal plant species. The occurrence data for each replicate was divided into a training group (70% of the sampled occurrence data for each plant species) and a test or validation group (30% of the sampled occurrence data for each plant species), using the bootstrap method. As the algorithms used are based on presence and pseudo-absence data, we configured the distribution models to select 500 pseudo-absences in grid cells that had less climatic suitability for the presence of the species (Barbet-Massin *et al.* 2012).

In total, 1800 distribution projections were built (species x scenarios x algorithms x climatic models), of which 450 refer to the current scenario and 1350 to future scenarios. The performance of the each of the models was evaluated using TSS (True Skill Statistics) and AUC (Area Under the Curve), which have already been used in other studies to evaluate plant distribution models in the Caatinga dry forest (Silva *et al.* 2020). The TSS and AUC are standard measures of goodness-of-fit for species distribution models (Allouche *et al.* 2006). TSS differentiates the overall accuracy of a model based on its random accuracy, providing a score between -1 and 1, with values close to 1 indicating optimal performance (Allouche *et al.* 2006). Values of TSS above 0.5 are considered satisfactory to inform the performance of the model. AUC values ranged from 0 to 1. When the accuracy is low, AUC values generally range from 0.5 to 0.7. Models with moderate accuracy exhibit AUC values between

0.7 and 0.9, while a high degree of accuracy is typically greater than 0.9 (Wakie *et al.* 2014).

Based on the ensemble method, we used consensus maps of habitat suitability for the medicinal plant species in each package and climate scenario analyzed through a PCA. In total, 100 consensus maps were generated, 10 referring to the current scenario and 90 referring to future scenarios (30 maps for each scenario, three maps per species). We combined the three maps of each species in each future scenario using the “Spatial Analyst Tools” function followed by “Cell Statistics - Overlay Statistic (Mean)” in ArcGIS 10.0 software (ESRI 2010). For analytical purposes, we defined suitable habitat areas as those with a high probability of occurrence ($\geq 80\%$, e.g., Silva *et al.* 2019, Li *et al.* 2020). Then, we cut all consensus maps to analyze the effects of climate change on the distribution of medicinal plant species in the Caatinga dry forest. The extent of suitable habitat was calculated separately from the maps generated for each species in each scenario. All modeling results were checked and edited using ArcGIS 10.0 software (ESRI 2010). The strong influence of the greater importance of climatic variables for defining the limits of occurrence of species suggests that the models generated capture biological factors that govern the persistence of the population in the environment (Searcy and Shaffer 2016). In the Results section, we set up a table stating the importance of predictor variables (e.g., Mweya *et al.* 2016; Aguirre-Gutiérrez *et al.* 2017; Wang *et al.* 2018) for the medicinal plant set in each scenario studied in the dry Caatinga dry forest.

As additional information, we investigated the pattern of species richness and composition of medicinal plants in each climate change scenario (SSP 2.45, SSP 3.70, SSP 5.85). For both, we use the resulting LPT (Lowest Presence Threshold) binary maps and calculated the species richness and composition (D’Amen *et al.* 2015). The species richness was calculated by combining/summing the presence of each medicinal plant species per cell of the binary maps (presence and absence) generated together with the consensus probability maps, producing a consensus map of taxonomic richness (e.g., Liu *et al.* 2005; Dubuis *et al.* 2011; Guisan and Rahbel 2011). The species composition was calculated based on the probability ranking rule, classifying the species in each assemblage based on the probability of occurrence obtained for each species (sum of the probability maps of occurrence of the species) and on the number of species per assemblage (map of species richness) (D’Amen *et al.* 2015). Species composition reduces species richness overprediction (for more details see D’Amen *et al.* 2015). We used the “Spatial Analyst Tools” function followed by “Cell Statistics - Overlay Statistic (Sum)” and “Cell Statistics - Overlay Statis-

tic (Range)” to access the species richness and composition, respectively, in ArcGIS 10.8 software (ESRI 2019). Prediction of species richness and composition based on the sum of predictions from species distribution models is as reliable and important as macroecological models (Dubuis *et al.* 2011; Guisan and Rahbel 2011, D’Amen *et al.* 2015), and can help identifying community assembly mechanisms (Grunié *et al.* 2020). It is worth mentioning that species distribution models are based on the fact that environmental conditions determine the species occurrence, not including additional processes [e.g., plant-plant interaction (e.g., competition), plant-animal interaction (e.g., pollination, dispersion)] in the predictions (Guisan and Zimmermann 2000).

RESULTS

The high AUC and TSS values indicate that the performance of all models have high quality, effectiveness, and greater proximity to the occurrence data, with AUC and TSS showing mean values of 0.78 and 0.7, respectively (Table 2). Comparing the current scenario with any future scenario, we observed that climate change may be associated with a reduction in areas of suitable habitats for seven of the 10 studied species and with an increase for four species in the Caatinga dry forest. Specifically, suitable habitats may be reduced by up to 2.71% for *Bauhinia cheilantha*, 7.53% for *Amburana cearensis*, 8.36% for *Operculina macrocarpa*, 8.83% for *Myracrodruon urundeuva*, 12.02% for *Anadenanthera colubrina*, 14.22% for *Neocalyptrocalyx longifolium* and 22.22% for *Operculina hamiltonii*; and increased for *Maytenus rigida* (2.81 – 4%), *Erythrina velutina* (2.91 – 6.52%) and *Cereus jamacaru* (0.76 – 7.88%) (Figures 2-4). Areas of suitable habitats may be reduced in the same proportion in the SSP 3.70 and SSP 5.85 for *N. longifolium*, about 14.22% and 14.07% respectively, in comparison to the current scenario (Figures 2 and 3I-L). Future areas of suitable habitat for *B. cheilantha* will likely be increased in the SSP 2.45 scenario (20.94%) and will likely be reduced in the SSP 3.70 and SSP 5.85 climate change scenarios in comparison to the current scenario (1% and 2.71%, respectively) (Figures 2 and 4M-P).

Comparing the three future climate change scenarios with the current scenario, reductions in areas with a high probability of occurrence may be more intense in the SSP 3.70 scenario for *N. longifolium*, *O. hamiltonii* and *A. cearensis*, and in the SSP 2.45 scenario for *O. macrocarpa*, *A. colubrina* (Figures 2-3) (Figures 2 and 4Q-T). Increases in areas with a high probability of occurrence will be more intense in the 2.45 scenario for *M. urundeuva*, *C. jamacaru*, *M. rigida*, *B. cheilantha*, and in the SSP 5.85 scenario for

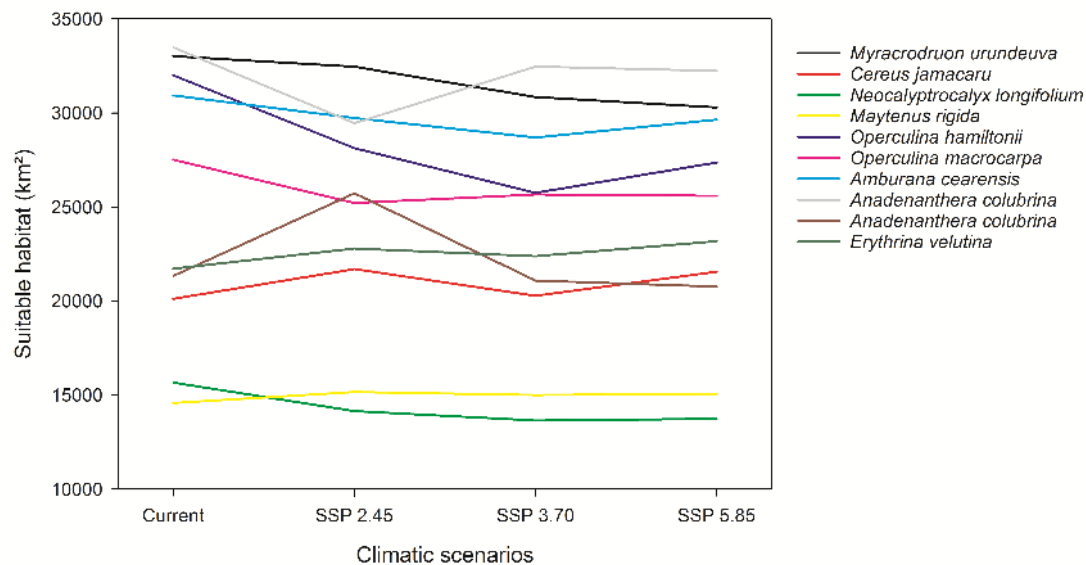


Figure 2. Potential changes in the future distribution (i.e., areas with probability of occurrence > 80%) of medicinal plant species native to the Caatinga dry forest in three scenarios of climate change (SSP 2.45, SSP 3.70 and SSP 5.85).

C. velutina (Figures 2-4).

Considering species richness, in total, we observed that the three future climate change scenarios (SSP 2.45, SSP 3.70 and SPP 5.85) show a reduction in species richness per grid cell of about 15.5% in the SSP 2.45 scenario, 12% in the SSP 3.70 scenario and 22% in the SSP 5.85 scenario (Figure 5). The maps of potential distribution of species richness show fewer species in the north and southeastern areas of the Caatinga dry forest, regardless of the climate change scenario (Figure 6A-D). Considering the species composition, one to four species can be distributed without any barriers to dissemination or competitive interactions in the three climate scenarios studied (Figure 6E-H).

The models generated and analyzed showed that annual precipitation and elevation had a high contribution in the current, SSP 3.70 and SSP 5.85 scenarios for all medicinal plant species native to the Caatinga dry forest (Table 3). The environmental variables elevation and precipitation of the coldest quarter had a high contribution in the SSP 2.45 (Table 3).

DISCUSSION

Our results indicate that climate change may distinctly affect areas of suitable habitats for medicinal plants in the Caatinga dry forest. Depending on the

climatic scenario, SSP 2.45, SSP 3.70 or SSP 5.85, suitable habitats for medicinal plants in the Caatinga dry forest may be increased or reduced. In total, contractions in areas of suitable habitats were observed in 70% of the analysed species, signalling that the effects of climate changes are species-specific. Expansions in suitable areas were observed for 30% of the studied species, refuting our hypothesis for these species. Furthermore, climate change may reduce, by up to 22%, the species richness of medicinal plants in the Caatinga dry forest. By affecting the extent of suitable habitats, species richness and composition, climate change may also negatively impact the provisioning of ecosystem services, such as natural medicines, in the Caatinga dry forest, since the majority of the medicinal species may exhibit a reduction in habitat suitability independently of the tested climate scenario.

Our results reinforce the idea that some species of medicinal plants are sensitive to climate change and partially corroborate recent evidence that climate change, independent of intensity, may negatively affect habitat suitability for native plant species in the Caatinga dry forest (e.g., Silva *et al.* 2019; Cavalcante *et al.* 2020). Seasonally dry tropical forests, such as the Caatinga, are sensitive to changes in climate since they are already at the threshold of temperature and water availability (e.g., Allen *et al.* 2017). In general, the few studies that address forecasting

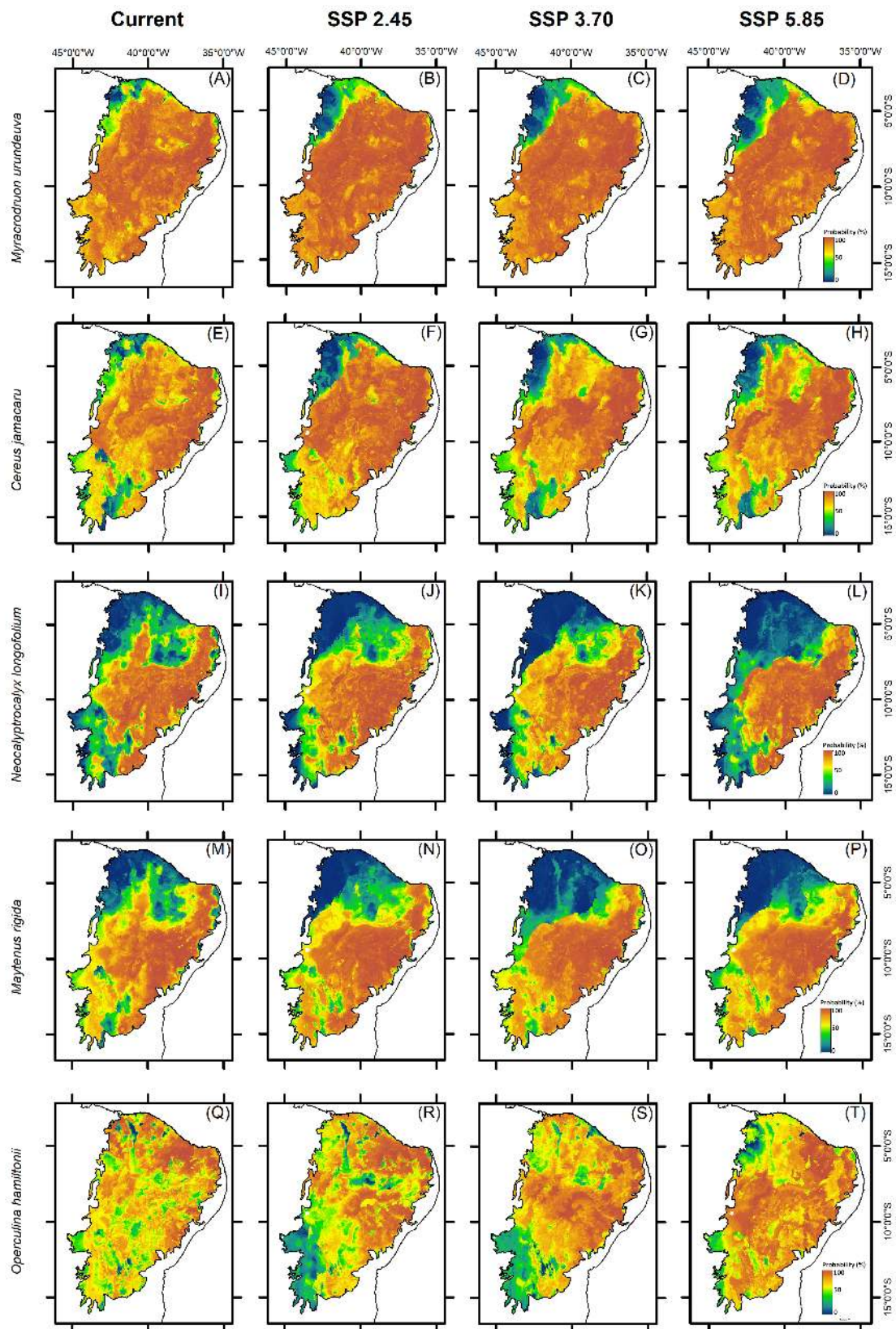


Figure 3. Geographical projection of suitable habitat for medicinal plants to the Caatinga dry forest in the present and two future scenarios (SSP 2.45, SSP 3.70 and SSP 5.85) for 2090 (average 2081 - 2100). *Myracrodruon urundeuva* (A-C), *Cereus jamacaru* (D-F), *Neocalyptocalyx longifolium* (G-I), *Maytenus rigida* (J-L) and *Operculina macrocarpa* (M-O).

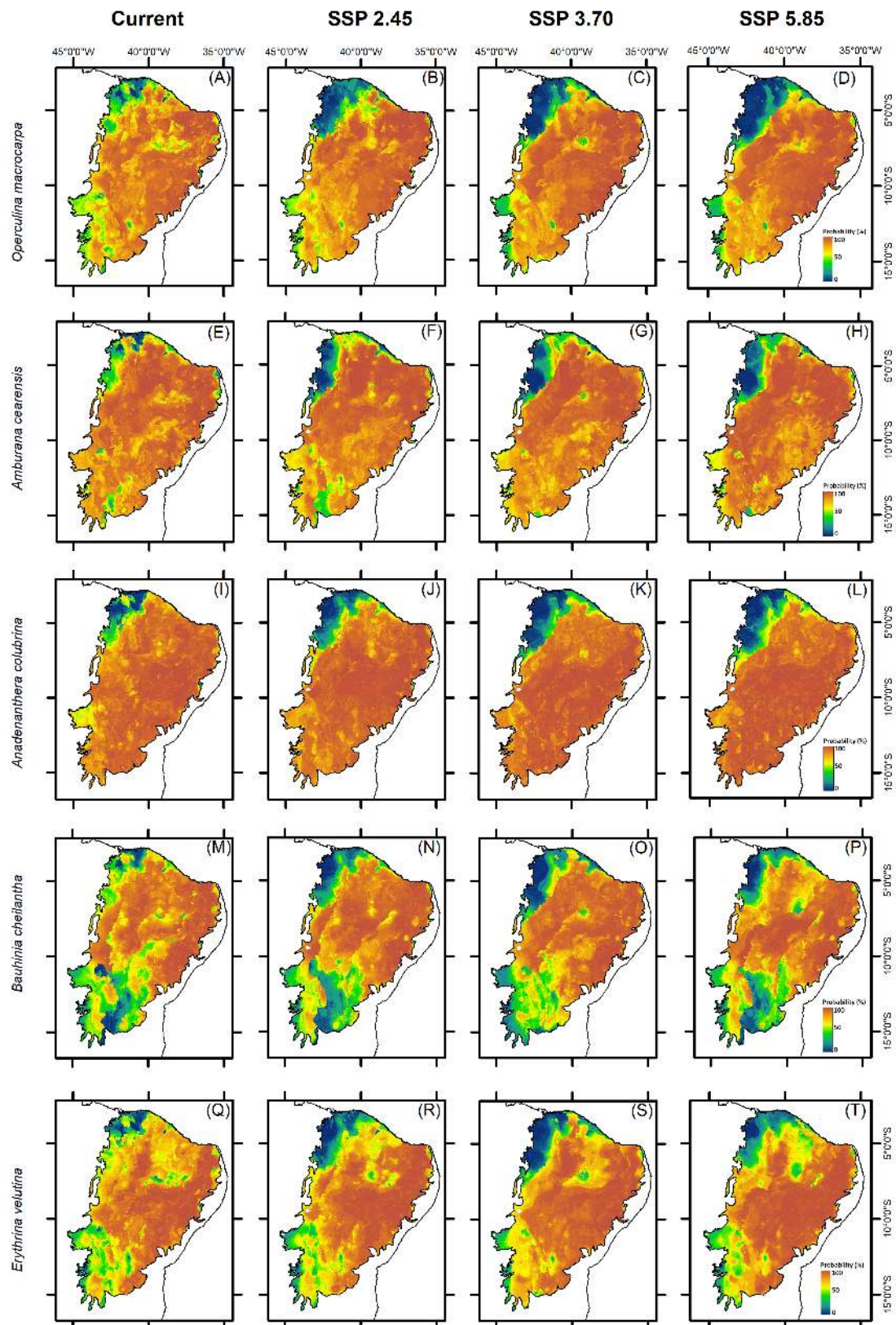


Figure 4. Geographical projection of suitable habitat for medicinal plants to the Caatinga dry forest in the present and three future scenarios (SSP 2.45, SSP 3.70 and SSP 5.85) for 2090 (average 2081 - 2100). *Operculina hamiltonii* (A-C), *Amburana cearensis* (D-F), *Anadenanthera colubrina* (G-I), *Bauhinia cheilantha* (J-L) and *Erythrina velutina* (M-O).

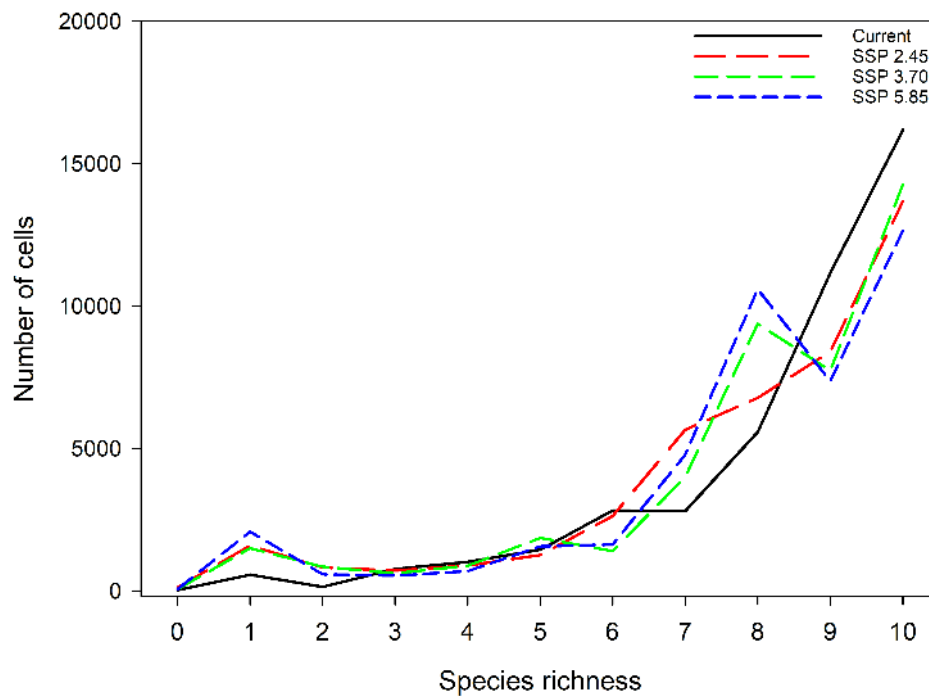


Figure 5. Richness of medicinal plants species in the Caatinga dry forest in the current and three future scenarios SSP 2.5, SSP 3.70 and SSP 5.85) for 2070 (average 2081 - 2100).

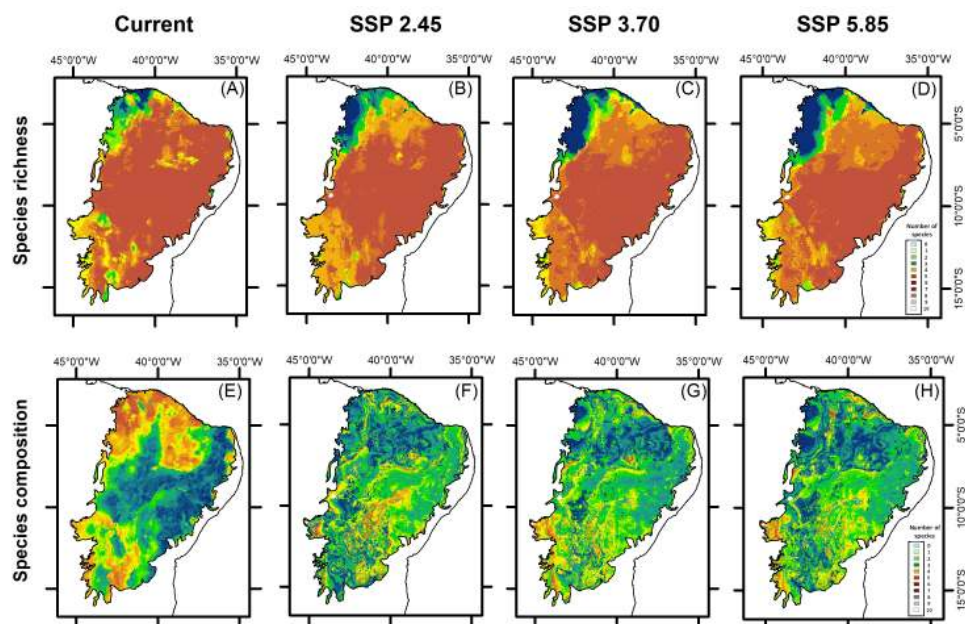


Figure 6. Distribution of species richness and composition of medicinal plants in the Caatinga dry forest in the current and three future scenarios SSP 2.5, SSP 3.70 and SSP 5.85) for 2090 (average 2081 - 2100).

plant responses to future climate change show relevant changes in the area of suitable habitat for medicinal plants occurring in tropical regions (e.g., Kanhum *et al.* 2013; Kaky and Gilbert 2016; Roy and Roy 2016) and temperate regions (e.g., Salick *et al.* 2009; Munt *et al.* 2016; Kumar *et al.* 2017a; Li *et al.* 2019). Climatic forecasts indicate that suitable habitats for plants in the Caatinga dry forest are likely to be reduced with increases in temperature and decreases in precipitation (Marengo *et al.* 2011; Andrade *et al.* 2017; Silva *et al.* 2019). More intense and negative impacts on the habitats are expected for plants bearing specialized reproductive strategies (such as dioecious or self-incompatible species, i.e., obligatory cross-pollination) and that are endemic to the Caatinga dry forest (Silva *et al.* 2019). On the other hand, it is expected that some species will be able to resist prolonged and intense drought since they have conservative water use strategies (Santos *et al.*, 2014). This resistance may increase the area of suitable habitat, as observed in this study for *C. jamacaru*, *M. rigida* and *E. velutina* with climate change.

Suitable habitats for medicinal plants native to the Caatinga dry forest may be reduced, increased or not changed by climate change. Complex patterns of suitable habitat change may be related to the fact that plants have different strategies that maximize water use. According to morphological, anatomical and ecophysiological studies, some species of dry tropical forests will be able to adapt to severe drought due to characteristics such as leaf loss and the presence of xylem that supports high negative pressure during drought, water storage capacity in the stem, deep roots, and high resilience to gas exchange, among others (Santos *et al.* 2014). Associated with these characteristics, the wide distribution in dry forests seems to favour the permanence of these species. *Cereus jamacaru*, for example, has high resistance to water stress and high temperatures (Meiado *et al.* 2010; Silva *et al.* 2020) and therefore is widely distributed and abundant in the Caatinga dry forest, including the driest areas (Meiado *et al.* 2010). Additionally, *E. velutina* is able to improve water use efficiency to compensate for water stress (Leite *et al.* 2022), being distributed in areas of Caatinga dry forest and Cerrado in Brazil (Martins 2020). Therefore, one could think that species with these traits would tend not to be impacted by future climate changes. However, these species, as well as others, present a wide variety of use and management strategies in social-ecological systems. One of the unknowns of climate change is that it must also alter people's behaviour, in that systems, so that the use of some plants can be drastically increased throughout their geographical distribution, as will be discussed further below. Studies suggest

that the loss of species (plants, mammals and birds, for example) as a consequence of climate change is a trend for dry tropical forests (e.g., Golicher *et al.* 2012; Hidas-Neto *et al.* 2019; Prieto-Torres *et al.* 2020; Pinedo-Escatel *et al.* 2021). The negative impact of reduced levels of precipitation and recurrent drought events on the species richness of medicinal plants in the dry Caatinga forest agrees with these predictions. The potential loss of species in southern and southeastern regions may directly reflect the pattern of use of medicinal plants by the inhabitants of these places, who depend on the forest for subsistence.

The intense exploitation of medicinal plants can cause local extinction by increasing the reduction in the geographical distribution of a given plant, independent of the climatic conditions (Svenning *et al.* 2009; Santos *et al.* 2014). Santos *et al.* (2017) evaluated 28 species of medicinal plants of the Caatinga dry forest for local importance and use, among other variables, concluding that seven species should have priority for conservation. *Amburana cearensis* and *Bauhinia cheilantha* are among the plants they indicate with high priority for conservation since they are severely used by rural communities, as they have medicinal and economic interest and are frequently reported in ethnobotanical studies. It is worth remembering that although some medicinal plants can adapt to changes in the climate (e.g., *Cereus jamacaru*, *M. rigida* and *E. velutina*) and resist human exploitation, the pharmaceutical properties may be altered. The effects of climate change on the quantity and quality of primary and secondary plant metabolites are still not well documented. However, studies indicate that high concentrations of CO₂ and temperature are able to alter the amount of secondary metabolites produced (e.g., Kumar *et al.* 2017; Holopainen *et al.* 2018; Jamloki *et al.* 2021). In this sense, increases in temperature and decreases in precipitation clutter the signaling cascade of metabolic pathways that regulate the production of secondary metabolites and a reduction in plant productivity (Gupta *et al.* 2019; see also Albergaria *et al.* 2020, 2021). Furthermore, we do not know how climate change will affect human behavioural patterns so that the intensity of use of a species can be increased due to environmental pressures on human populations (e.g., Applequist *et al.* 2020). A factor that aggravates this situation, especially in the semiarid region, is that most of the plants used in the Caatinga dry forest are multipurpose species (Albuquerque *et al.* 2009). This implies that in addition to medicinal use, they can be used for food, fuel, house building and other architectural constructions. Therefore, future studies of the effects of climate change on medicinal plants should also con-

sider the patterns of use of these species and how they are modulated by social-ecological variables (e.g., Albuquerque *et al.* 2019).

By changing areas of suitable habitats, species richness and composition of medicinal plants in the Caatinga dry forest, climate change may compromise the ecosystem functions and services provided by them. The functions are mainly associated with ecological interactions, such as pollination and seed dispersion, while the ecosystem service is represented by the medicinal use of these plants. As a main consequence, it is expected that there will be important changes in ecological interactions, including the structure of interaction networks (Tylianaskis *et al.* 2008), phenological synchrony (Memmott *et al.* 2007) and geographic distribution of animal species (Oliveira *et al.* 2012; Costa *et al.* 2018). Pollination and dispersion are considered key processes for maintaining plants in the ecosystem (Strykstra *et al.* 2002; Kremen *et al.* 2007) and, therefore, are essential for the provision of ecosystem services, such as food, timber, medicinal and nutrient cycling (Wenny *et al.* 2011; IPBES 2016; Evangelista-Vale *et al.* 2021). In this sense, associated with the loss of suitable habitats for *M. urundeuwa*, *N. longifolium*, *A. cearensis*, *A. colubrina* and *B. cheilantha*, these species have an even worse scenario, as they are obligatory outcrossing species, therefore depending on pollinators for their reproduction (Table 1). Accordingly, they may experience greater restrictions for their future permanence in some areas of the Caatinga dry forest. Even the increase in areas of suitable habitats for *C. jamacaru*, *E. velutina* and *M. rigida* is not a guarantee of permanence for these species. *Cereus jamacaru* and *M. rigida* also obligatory depend on animals (specialist, in the case of *C. jamacaru*) for their reproduction (Table 1). On the other hand, *Erythrina velutina*, despite showing genetic self-compatibility, is pollinated by hummingbirds, a vector that is also specialist (Table 1) and which may show a reduction in areas of probable occurrence in the Caatinga dry forest, as projected by Centeno-Alvarado *et al.* (2022). All three species still depend on animals to disperse their seeds (Table 1). Thus, the services provided by medicinal plants to native human populations, including improved quality of life, income generation in the local economy and cultural value (Klein *et al.* 2008), may be altered. Future reductions in suitable habitat for *M. urundeuwa*, *N. longifolium*, *O. hamiltonii*, *O. macrocarpa*, *A. cearensis* and *B. cheilantha* will reduce the possibility of treating diseases such as inflammation in general, renal, hepatic and respiratory problems, cardiovascular problems, helminthiasis, lung inflammation, diabetes, spinal problems, nervous disturbances, calmativity, and odontalgia (Table 1S1), mainly in

the north and southeastern areas of the Caatinga dry forest. Specifically, the possibility of treating diseases such as anemia and blood thinner will be negatively impacted, since the other species of medicinal plants analyzed in this study are not used for these purposes. In contrast, the increase in area of probable occurrence of *C. jamacaru*, *M. rigida* and *E. velutina* may increase the chances of treating renal problems, hepatic problems and insomnia in particular. Therefore, low-income communities in the Caatinga dry forest that use plants intensively for popular medicine (Albuquerque *et al.* 2017) may be negatively impacted, since in most cases, these plants are the only available resource for the treatment of diseases.

Our results indicate that precipitation is the most relevant variable to the distribution of medicinal plant species in the Caatinga dry forest. Water availability is a limiting factor for the occurrence of plants in tropical dry forests (Pennington *et al.* 2000; Esquivel-Muelbert *et al.* 2016; Chaturvedi and Raghubanshi 2018), such as the Caatinga dry forest (Silva *et al.* 2017b). Precipitation influences several ecological processes, such as flowering and fruiting, seed germination, and seedling growth (e.g., Khurana and Singh 2001; Bustamante-Becerra *et al.* 2014; Silva *et al.* 2020), and consequently can alter the composition of species in the community (Segura *et al.* 2002; Esquivel-Muelbert *et al.* 2016; Hiltner *et al.* 2016). However, our species distribution modelling study uses only environmental variables (climatic and edaphic) and occurrence data for medicinal plant species, and it would also be interesting for future studies to consider other ecological parameters that drive species distribution, such as edaphic factors and interaction with animal pollinators and dispersers, important agents in the reproduction of angiosperms.

CONCLUSION

Our results highlighted that climate change may exert distinct impacts on the area and distribution of suitable habitat, in addition to reducing the richness of medicinal plant species in the Caatinga dry forest, acting directly in the provision of ecosystem services, such as the provisioning of natural medicines for rural human populations. Regardless of the climate change scenario, the conservation of the biodiversity of the Caatinga dry forest still presents challenges. Therefore, conservation strategies are needed for species of medicinal plants native to the Caatinga dry forest and with a high relative importance index, especially those with endangered conservation status. These strategies may also contribute to the maintenance of ecosystem services provided by medicinal plants in the Caatinga dry forest.

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DATA AVAILABILITY

The authors confirm that the data supporting the findings of this study are available within the article's supplemental material.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

CONTRIBUTION STATEMENT

Conceptualization: JLSS, AVL, UPA.

Data curation: JLSS.

Formal analysis: JLSS, OCN.

Investigation: JLSS, OCN.

Methodology: JLSS, OCN, AVL, UPA, MT.

Visualization: JLSS.

Writing - original draft: JLSS.

Writing - review & editing: JLSS, OCN, AVL, UPA, MT.

SUPPLEMENTARY DATA

Data associated with: Climate change will likely threaten areas of suitable habitats for the most relevant medicinal plants native to the Caatinga dry forest. [<https://doi.org/10.5281/zenodo.6792819>]

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Table 1. Reproductive traits of the medicinal plant species native to the Caatinga dry forest that exhibit high relative importance index ($RI \geq 1.5$). Traits marked in bold are considered highly specialized. [Hm = Hermaphrodite; D= Dioecious; M= Monoecious; SI= self-incompatible; SC= self-compatible; OC= outcrossing (obligatory cross pollination)].

Families/Species	Pollination systems ^a	Specialist or generalist Pollination System ^b	Sexual system ^c	Reproductive system ^d	Dispersal mode ^e	Relative importance index ^f	References
Anacardiaceae							
<i>Myracrodruon urundeuva</i>	Diverse small insects ¹	G	D ²	D (OC) ²	Wind ³	2.0	¹ Soares et al. 2014; ² Machado et al. 2006; ³ Carvalho 2003
Cactaceae							
<i>Cereus jamacaru</i>	Sphingids ¹	S	Hm ²	SI (OC) ³	Animal ⁴	1.7	¹ Zanina 2013; Personal observations; ² Machado et al. 2006; ³ Rafiana et al. 2021; ⁴ Silva & Rodal 2009
Capparaceae							
<i>Neocalyptocalyx longifolium</i>	Bats ¹	S	M ²	SI (OC) ²	Autochory ³	1.5	¹ Machado & Lopes 2004; ² Machado et al. 2006; ³ Silva & Rodal 2009
Celastraceae							
<i>Maytenus rigida</i>	Diverse small insects ¹	G	D ²	D (OC) ²	Animal ³	1.9	¹ Carvalho 2008; ² Leite & Machado 2010; ³ Silva & Rodal 2009
Convolvulaceae							
<i>Operculina hamiltonii</i>	Bees ¹	S	Hm ¹	-	Autochory ²	1.6	¹ Staples et al. 2020; ² Peres 2016
<i>Operculina macrocarpa</i>	Bees ¹	S	Hm ¹	-	Autochory ²	1.6	¹ Staples et al. 2020; ² Peres 2016
Leguminosae							
<i>Amburana cearensis</i>	Moths ¹	G	Hm ²	SI (OC) ¹	Wind ³	2.0	¹ Barral 2018; ² Machado et al. 2006; ³ Leal et al. 2003
<i>Anadenanthera colubrina</i>	Bees ¹	G	M ¹	SI (OC) ²	Autochory ³	1.6	¹ Borges et al. 2017; ² Borges 2010; ³ Griz & Machado 2001
<i>Bauhinia cheilantha</i>	Bats ¹	S	Hm ²	SI (OC) ³	Autochory ⁴	1.7	¹ Quirino & Machado 2014; ² Machado et al. 2006; ³ Leite 2006; ⁴ Machado et al. 1999
<i>Erythrina velutina</i>	Hummingbirds and birds ¹	S	Hm ²	SC ³	Animal ⁴	1.5	¹ Rocco & Sazima; ² Machado et al. 2006; ³ Ribeiro 2011; ⁴ Griz & Machado 2001

^aCategories according to Girão et al. (2007), Lopes et al. (2009), Faegri and van der Pijl (1979); ^bClassification sensu Kang & Bawa (2003); ^cAccording to Bawa (1980), Endress (1994), Proctor et al. (1996); ^dClassification according to Richards (1997); ^eCategories according to Pijl (1982); ^fValues from Albuquerque et al. (2007).

Table 2. Adjustments between the sample points of medicinal plant species native to the Caatinga dry forest and climatic scenarios for the current period (average for 1970 - 2000) and three future scenarios for 2090 (average for 2081 - 2100): SSP 2.45, SSP 3.70 and SSP 5.85.

Species	Climate scenarios	AUC		TSS	
		Mean	SD	Mean	SD
<i>Myracrodruon urundeuva</i>	Current	0.86	0.01	0.76	0.03
	2.45	0.89	0.006	0.75	0.01
	3.70	0.89	0.005	0.75	0.01
	5.85	0.89	0.006	0.78	0.01
<i>Cereus jamacaru</i>	Current	0.86	0.009	0.73	0.01
	2.45	0.89	0.008	0.76	0.01
	3.70	0.89	0.008	0.81	0.007
	5.85	0.88	0.007	0.86	0.01
<i>Neocalyptrocalyx longifolium</i>	Current	0.87	0.007	0.81	0.01
	2.45	0.88	0.005	0.81	0.01
	3.70	0.89	0.005	0.79	0.01
	5.85	0.88	0.006	0.81	0.01
<i>Maytenus rigida</i>	Current	0.93	0.009	0.75	0.02
	2.45	0.94	0.007	0.85	0.01
	3.70	0.93	0.006	0.83	0.01
	5.85	0.94	0.01	0.85	0.01
<i>Operculina hamiltonii</i>	Current	0.78	0.02	0.71	0.03
	2.45	0.79	0.02	0.74	0.04
	3.70	0.80	0.01	0.72	0.04
	5.85	0.87	0.02	0.75	0.04
<i>Operculina macrocarpa</i>	Current	0.88	0.01	0.77	0.02
	2.45	0.88	0.01	0.72	0.03
	3.70	0.89	0.01	0.77	0.02
	5.85	0.89	0.009	0.76	0.02
<i>Amburana cearensis</i>	Current	0.89	0.01	0.85	0.02
	2.45	0.90	0.006	0.75	0.01
	3.70	0.89	0.007	0.84	0.01
	5.85	0.89	0.006	0.80	0.02
<i>Anadenanthera colubrina</i>	Current	0.87	0.003	0.81	0.009
	2.45	0.88	0.003	0.72	0.009
	3.70	0.89	0.003	0.74	0.008
	5.85	0.88	0.003	0.74	0.009
<i>Bauhinia cheilanta</i>	Current	0.89	0.009	0.70	0.01
	2.45	0.88	0.01	0.72	0.01
	3.70	0.89	0.009	0.82	0.01
	5.85	0.89	0.006	0.78	0.01
<i>Erythrina velutina</i>	Current	0.86	0.01	0.79	0.03
	2.45	0.90	0.01	0.76	0.02
	3.70	0.90	0.01	0.83	0.03
	5.85	0.90	0.01	0.83	0.02

Table 3. Summary of principal component analysis for environmental variables used in modelling the distribution of medicinal plant species native to the Caatinga dry forest including variable loads for principal components 1-2.

Scenarios	Axes	Variables					Elevation
		Temperature seasonality	Annual precipitation	Precipitation of wettest quarter	Precipitation of warmest quarter	Precipitation of coldest quarter	
Current	PC1	-0.495	0.678	0.242	0.103	0.215	-0.634
	PC2	0.112	-0.546	-0.196	-0.101	-0.180	-0.772
SSP 2.45	PC1	-0.116	0.263	0.223	-0.292	0.118	-0.421
	PC2	-0.258	-0.359	0.188	0.284	-0.379	-0.316
SSP 3.70	PC1	-0.178	0.756	0.290	0.215	0.302	-0.439
	PC2	-0.344	-0.37	-0.153	0.32	-0.394	-0.887
SSP 5.85	PC1	-0.121	0.769	0.297	0.154	0.302	-0.418
	PC2	-0.400	-0.365	-0.151	-0.326	-0.142	-0.902