



## ECOSYSTEMS

# Impacts of climate change on the potential distribution of epiphytic cacti in the Caatinga biome, Brazil

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**Abstract:** The Caatinga biome is the largest dry tropical forest region in South America as well as one of the most vulnerable regions in the world to the climate changes forecast for this century. Climate forecasts for the biome include increased air temperature, reduced rainfall and aridization. This biome does not have a homogeneous landscape; instead it has several rainforest enclaves. This article describes a study to model the potential distribution of four epiphytic cactus species (*Epiphyllum phyllanthus* (L.) Haw., *Rhipsalis floccosa* Salm-Dyck ex Pfeiff., *Rhipsalis lindbergiana* K. Schum and *Rhipsalis russellii* Britton & Rose.) in the biome under future climate scenarios and traces out a prognosis for the enclaves and the biome. For that purpose, we used the MaxEnt modeling method, considering two future time intervals (2041-2060 and 2061-2080) and the interval 1961-1990 for the current situation, with the RCP4.5 and 8.5 scenarios. The projections for future potential distribution showed a spatial contractions greater than 88% found in the areas of high potential presence for the target species throughout the biome and in all the scenarios. The results strengthen the expectation of aridization in the Caatinga biome, with the loss or shrinkage of rainforest enclaves as time progresses.

**Key words:** Climatic refuge, maxent, modeling, seasonally dry tropical forest.

## INTRODUCTION

It is well known that the topic of climate change is gaining relevance among the scientific community and has definitively entered the agenda of international political discussions, due to the potential negative impacts on human quality of life and biodiversity. The relevance of this phenomenon is supported by a wealth of evidence published in recent years, confirming the existence of various global climate changes with impacts on all continents and oceans (IPCC 2013, 2014a, b, 2018).

With respect to the impacts on biodiversity, there is scientific consensus that climate change is one of the most significant factors that will

induce extinction of species until the end of the century (CBD 2016), with various climate change components already threatening the survival of species and the quality of ecosystems and biomes (Bellard et al. 2012).

Brazil stands out among countries for its huge ecological diversity. As such, it has been attracting growing interest from researchers regarding the effects of climate change on its biodiversity. Among the initiatives in this line, we can mention the First National Evaluation Report on Climate Change (PBMC 2014a, b), which presented predictions for rising air temperature and greater frequency of extreme climate events throughout the country, with significant negative impacts on all its biomes.

Inside of Brazil is located the Caatinga biome, the largest tropical dry forest region in South America (Silva et al. 2017). Along with the Amazon biome, it is considered one of the world's most vulnerable ecological regions to the climate changes forecast for this century (Baettig et al. 2007, Santos et al. 2014, Seddon et al. 2016). Among the projections for the Caatinga biome is aridization (increased number of months with water deficit) (Marengo 2008, 2014, Sales et al. 2015, Lacerda et al. 2016, Marengo et al. 2017). Another is that the air temperature at the surface will increase by up to 4 °C by the end of this century in the most critical scenario (Torres et al. 2017). Regarding precipitation, the forecast is for a reduction by 2100, although this projection is considered the most uncertain (Sales et al. 2015, Torres et al. 2017). All these forecasts taken together are reason for concern, especially about the continuing adequacy of habitats. Some studies have found indications of loss of this environmental adequacy for plant species in the Caatinga biome due to climate change projections (Rodrigues et al. 2015, Silva et al. 2019, Cavalcante et al. 2020, Simões et al. 2020).

The Caatinga ecological region is dominated by seasonally dry tropical forest (SDTF) (Pennington et al. 2009), but the SDTF is not a totally homogeneous landscape, because it contains enclaves of moist tropical forests that form veritable islands, with more amendable temperatures and higher rainfall due to the elevated terrain, in contrast to the lowlands covered by SDTF (Andrade-Lima 1982, Tabarelli & Santos 2004, Souza & Oliveira 2006, Santos et al. 2007). These enclaves, because of their distinctive environmental conditions of SDTF, sustain a greater diversity of plants and function as refuges for many species (Ab'Sáber 2003, Cavalcante 2005, Silva et al. 2014, Lopes et al. 2017).

In these rainforest enclaves, the native epiphytic cactus species can be valuable representatives, since knowledge of the geographic distribution and redistribution of this functional group can shed light on the possible impacts of climate change on the adequacy of habitats. Some studies have modeled functional groups to use them as bioindicators (Rodrigues et al. 2015, Oke & Hager 2017, Silva et al. 2019). A natural question thus arises: Can modeling of the future potential distribution of a group of native epiphytic cacti indicate losses of rainforest enclaves and improve the prognosis for aridization of the Caatinga biome during this century?

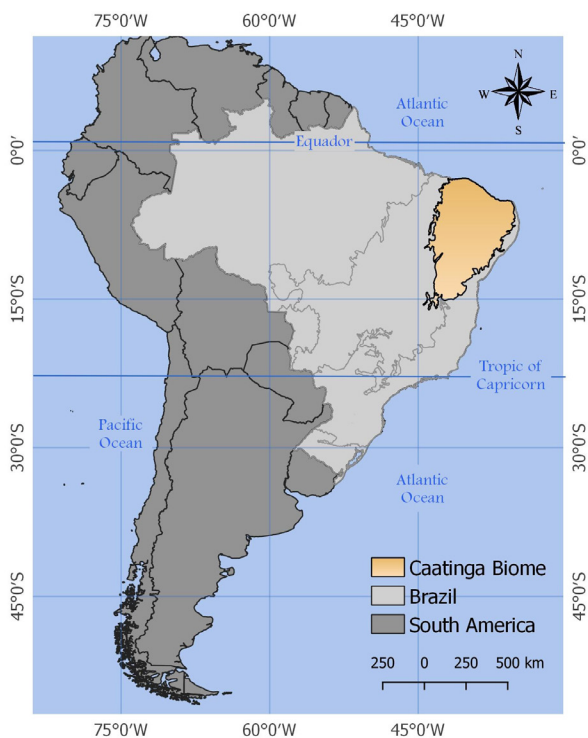
In this context, modeling the potential distribution of species is a useful tool to forecast the impacts of climate change on species in landscapes undergoing transformation. According to Hijmans & Elith (2017), the objective of species distribution modeling is to estimate the similarity of conditions of any area with the conditions of known areas of occurrence (or not) of a phenomenon. A common application of this method is to predict the ranges of species with climate data as predictors. Hence, species distribution modeling can provide probabilistic forecasts of where a given species may or may not be present, where the estimated area represents the potential distribution of the target species, based on its environmental preferences and constraints (Guisan & Thuiller 2005, Elith & Leathwick 2009, Franklin & Miller 2009).

Based on these observations, the objective of this study was to model the potential distribution of four epiphytic cactus species native to the Caatinga biome under future scenarios and to trace out a prognosis for the rainforest enclaves and the entire biome in this century.

## MATERIALS AND METHODS

### Description of the study area

The Caatinga biome covers 844,453 km<sup>2</sup>, or 10 % of Brazil's territory (IBGE 2004), and is almost all located in the country's Northeast region (Figure 1). According to the Köppen classification, it has a semiarid climate - BSh (Alvares et al. 2014). Because it is entirely located between the Equator and Tropic of Capricorn (3° to 18° South), it receives abundant sunlight throughout the year, with average annual temperatures ranging between 25° and 30°C (Sampaio 2003). The rainfall, on the other hand, varies widely in time and space, fluctuating on average from 300 to 1,000 mm a year (Reddy 1983). The dry season lasts 7 to 10 months, virtually without rainfall (Prado 2003). There are three main precipitation systems that affect the biome: the Intertropical Convergence Zone (ITCZ) in the north, the Easterly Wave Disturbances along the east coast, and Cold Fronts in the south (Andrade et al. 2017).



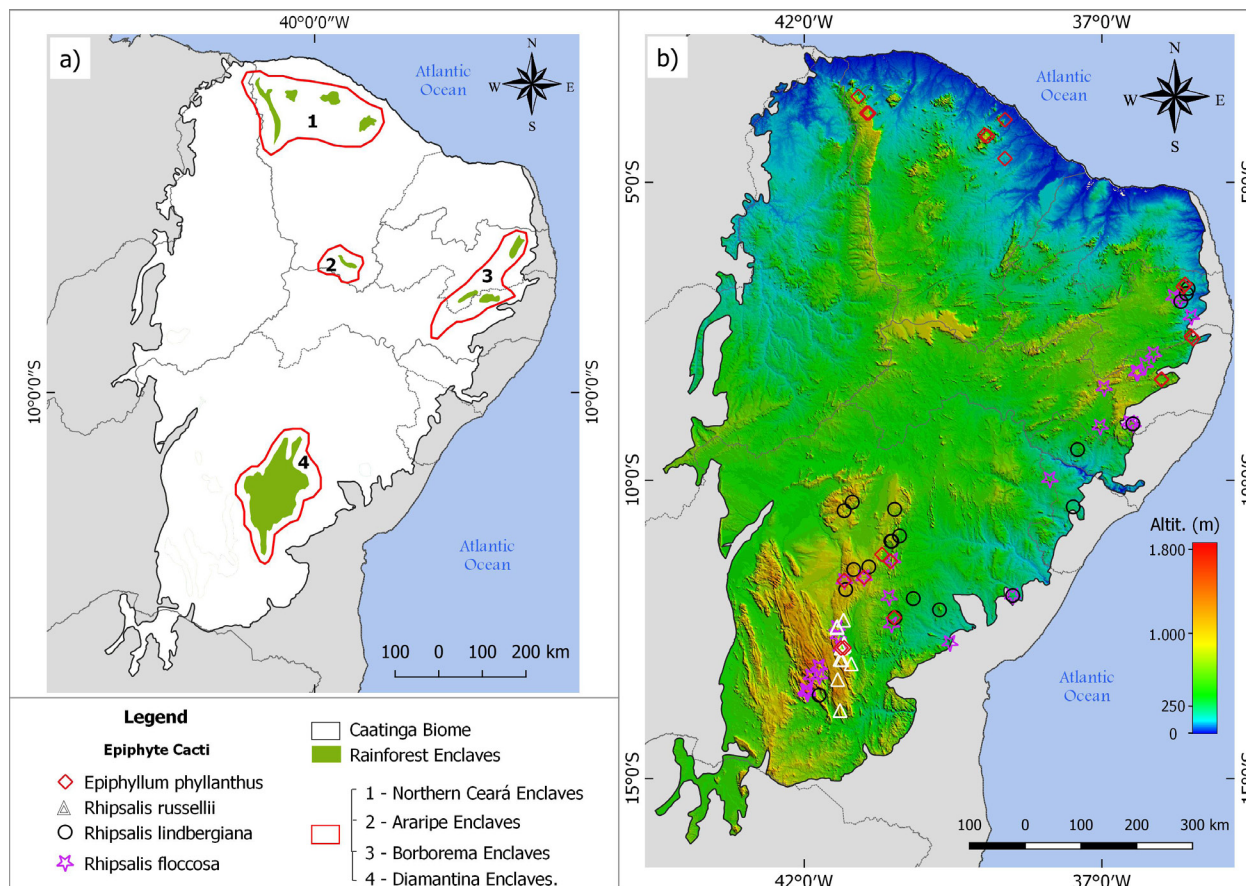
**Figure 1.** Location of the Caatinga biome.

In this extensive ecological region, the predominant vegetation is classified as seasonally dry tropical forest (SDTF) (Pennington et al. 2009), which is subject to a prolonged dry season, resulting in deciduous vegetation (Prado 2003). However, the SDTF is interspersed with rainforest enclaves at higher altitudes. These forests are recognized as islands that remain green throughout the year, acting as climate refuges of the Atlantic Forest (Tabarelli & Santos 2004, Cavalcante 2005, Neves et al. 2017, Silveira et al. 2019).

The morphostructural aspects of the reliefs play a fundamental role for these enclaves. They are associated with the high-altitude mesoclimate found in areas of crystalline massifs (granitic or metamorphic) and sedimentary plateaus (Souza & Oliveira 2006). For the analysis here, as described by Silveira et al. (2019), the rainforest enclaves in the biome were grouped into four sets: Northern Ceará; Borborema Plateau, Araripe Complex; and Eastern Chapada Diamantina (Figure 2a).

### Species selected

Of the 94 known cactus species present in the Caatinga biome, seven are true epiphytic species (Flora do Brasil 2020). Among these seven species, we selected four for this study: *Epiphyllum phyllanthus* (L.) Haw.; *Rhipsalis floccosa* Salm-Dyck ex Pfeiff.; *Rhipsalis lindbergiana* K. Schum; and *Rhipsalis russellii* Britton & Rose. The choice of true epiphytic cacti was first based on the particularity that these plants only occur in rainforest areas (Braun & Hofacker 2006), second on the possibility of tracing parallels as indicators for other species having similar demands in the ecological region, and third (but not less important), on the sufficient quantity and quality of biotic and geographic data available, as needed for the modeling. The four selected cactus species



**Figure 2. a) Location of the rainforest enclaves of the Caatinga biome; b) Records of the presence of the true epiphytic cacti selected.**

form a functional group that commonly occurs in moist areas that are strongly regulated by the climate (Taylor & Zappi 2004) (Fig. 2a, b).

**Modeling and simulation**

The species distribution modeling was carried out with the Maximum Entropy Algorithm (MaxEnt), version 3.4.1 (Phillips et al. 2006, 2018). It is a method developed to rely only on presence data and has performed well in previous studies, even with a small number of samples (Wiszniewski et al. 2008, Van Proosdij et al. 2016). For MaxEnt’s choice we took into account recommendations by Rangel & Loyola (2012).

The presence records of the species, identified by decimal geographic coordinates, were obtained from two online databases: the Global Biodiversity Information Facility (GBIF

2017) and the SpeciesLink (2018). These records were checked to remove redundant and spatially correlated ones. The result was a high-quality database containing 20, 37, 20 and 14 records of the presence of *E. phyllanthus*, *R. floccosa*, *R. lindbergiana* and *R. russellii*, respectively, for a total of 91 points (Figure 2b), which were modeled together as a single group.

The climate variables used, derived from temperature (11) and precipitation (8), were obtained from the WorldClim 1.4 (2018) (Hijmans et al. 2005), with spatial resolution of 30 arc-seconds (~1 km). Besides these, we also used topographic variables (3) obtained by remote sensing, collected from the Ambdata database (INPE 2018), with the same spatial resolution as the others. Some studies have indicated that models improve substantially with the inclusion



of remotely detected variables in relation to those relying only on directly measured climate variables (Pearson et al. 2004).

To reduce the possible errors caused by correlation of the variables, we applied principal component analysis (PCA) to the initial set of 22 variables, to select the eight that were most independent (correlation < 0.7) and with highest predictive power (Cruz-Cárdenas et al. 2014). The chosen variables and their respective codes were: Bio2 – monthly mean daily temperature range; Bio3 – isothermality; Bio5 – maximum temperature of the warmest month; Bio12 – annual precipitation; Bio14 – precipitation of the driest month; Bio19 – precipitation of the coldest quarter; Ele – elevation; and Dir – direction of slopes.

For future climate conditions, we used data from the general circulation model HadGEM2-ES, considering the time intervals 2041-2060 and 2061-2080, centered respectively at 2050 and 2070 (Hijmans et al. 2005), and the greenhouse gas concentration scenarios RCP4.5 and 8.5 (Van Vuuren et al. 2011) of the CMIP5. For the present scenario, we used the period 1960-1990 (Hijmans et al. 2005).

The background points were extracted from the area corresponded to the minimum convex polygon including all the presence records observed, plus a radius of 100 km (Vanderwal et al. 2009), while the final models were projected for the current extension of the Caatinga biome, considered previously as the area accessible to the target species over the relevant time period (Barve et al. 2011).

All told, we generated five models, one current and four for future scenarios. Each model resulted in an average of 20 replications, in which 25% of the points were separated for statistical testing, with replacement at the end of each replication by the bootstrap method. The output of the models can be interpreted

as habitat suitability indices for the selected species (Merow et al. 2013).

To assess the precision of the models, we used the area under the receiver operating characteristic curve (AUC). AUC values near 1 represent excellent performance, while values near 0.5 indicate the model is near a random classification (Elith et al. 2006). Although there are other techniques to evaluate performance, such as those proposed by Allouche et al. (2006) and Warren et al. (2014), the AUC is better to assess models involving only presence data (Merow et al. 2013). To set the parameters for the AUC values, we calculated 99 null models, as recommended by Raes & Ter Steege (2007).

The potential distribution maps of the target species were prepared with the QGIS 3.2.3 (2018) and included five potential classes: null potential or totally unsuitable area (0.0-0.01); low potential (0.01-0.25); moderate potential (0.25-0.50); good potential (0.50-0.75); and high potential, or highly suitable area (> 0.75). This classification was adapted from Yang et al. (2013). Based on the maps, we calculated the areas occupied in the current climate conditions, as well as the expanded or contracted areas in the future climate scenarios.

## RESULTS

The potential distribution models of the target species in the current and future climate scenarios performed well, with AUC values higher than 0.89 (Table I). The maximum AUC of the null models

**Table I. AUC values of the final models.**

Climate status	Time intervals	AUC
Current	1961-1990	0.89
RCP4.5	2041-2060	0.91
	2061-2080	0.89
RCP8.5	2041-2060	0.90
	2061-2080	0.90

with random samples was 0.67 with a confidence interval of 95%, confirming the accuracy of the models.

Of the set of eight environmental variables used, those that made the largest contribution to construction of the models were: precipitation in the driest month (Bio14) with 36%; maximum temperature in the hottest month (Bio5) with 26%; total annual precipitation (Bio12) with 20%; and elevation (Ele) with 8%. Together, these four variables contributed 90% to construction of the models, The other variables together contributed 10%, with the variable monthly mean daily temperature range (Bio2) having the smallest contribution, only 1% (Table II).

With respect to the potential presence classes of the target species in the Caatinga biome, the current habitats with high potential (>0.75) were found to cover 10,392 km<sup>2</sup>, or 1.2% of the biome’s total area (844,453 km<sup>2</sup>). The areas with good (0.50-0.75) and moderate potential (0.25-0.50) corresponded to 15,877 km<sup>2</sup> (1.9%) and 40,329 km<sup>2</sup> (4.8%), respectively. The low potential class (0.01-0.25) covered the largest area, of 440,820 km<sup>2</sup>, or 52.2%. Finally, the null potential class (0.0-0.01) covered the second largest area, of 319,056 km<sup>2</sup>, or 37.8% of the biome’s total area (Table III, Figures 3a and 4a).

The projected areas of the biome for future climate change scenarios (Table III, Figures 3b, c and 4b, c), in turn, showed significant and progressive contractions of areas with high potential (>0.75) in relation to the same areas in the current climate condition. These contractions ranged from 88.8% in the least critical scenario (RCP4.5/2050) to 99.7% in the most critical and longest range scenario (RCP8.5/2070), with almost total loss of high potential areas. The areas with good potential (0.50-0.75) followed the same contraction trend, varying from 77.4% in scenario RCP4.5/2050 to 98% in scenario RCP8.5/2070. The areas with moderate potential (0.25-0.50) showed similar contractions to those of the previously mentioned classes, with losses under the most critical climate condition (RCP8.5/2070) of 95.6% of the original areas. The low potential class (0.01-0.25) also would be subject to progressive contraction, but with smaller losses than in scenario RCP8.5/2070, of around 50%. Finally, in contrast to the other classes, the class with null potential (0.0-0.01), where the species would be absent with the greatest degree of certainty, showed strong and progressive expansion during the years in the different future climate scenarios, reaching expansion of 90.3% in 2070 in the most critical condition.

**Table II. Average percent contribution of the variables to the model.**

Variable	Climate Status					Média
	Current	RCP4.5/2050	RCP4.5/2070	RCP8.5/2050	RCP8.5/2070	
Bio14	36.8	30.6	39.9	34.8	37.5	35.9
Bio5	25.3	28.6	21.6	26.7	25.4	25.6
Bio12	18.7	21.9	19.2	22.1	18.1	20.0
Ele	8.3	6.8	9.3	5.8	8.9	7.8
Dir	5.2	7.3	5.6	5.3	5.1	5.7
Bio3	2.6	2.4	1.9	2.9	1.9	2.3
Bio19	2.4	1.1	1.5	1.2	2.0	1.6
Bio2	0.7	1.4	0.9	1.2	1.0	1.0

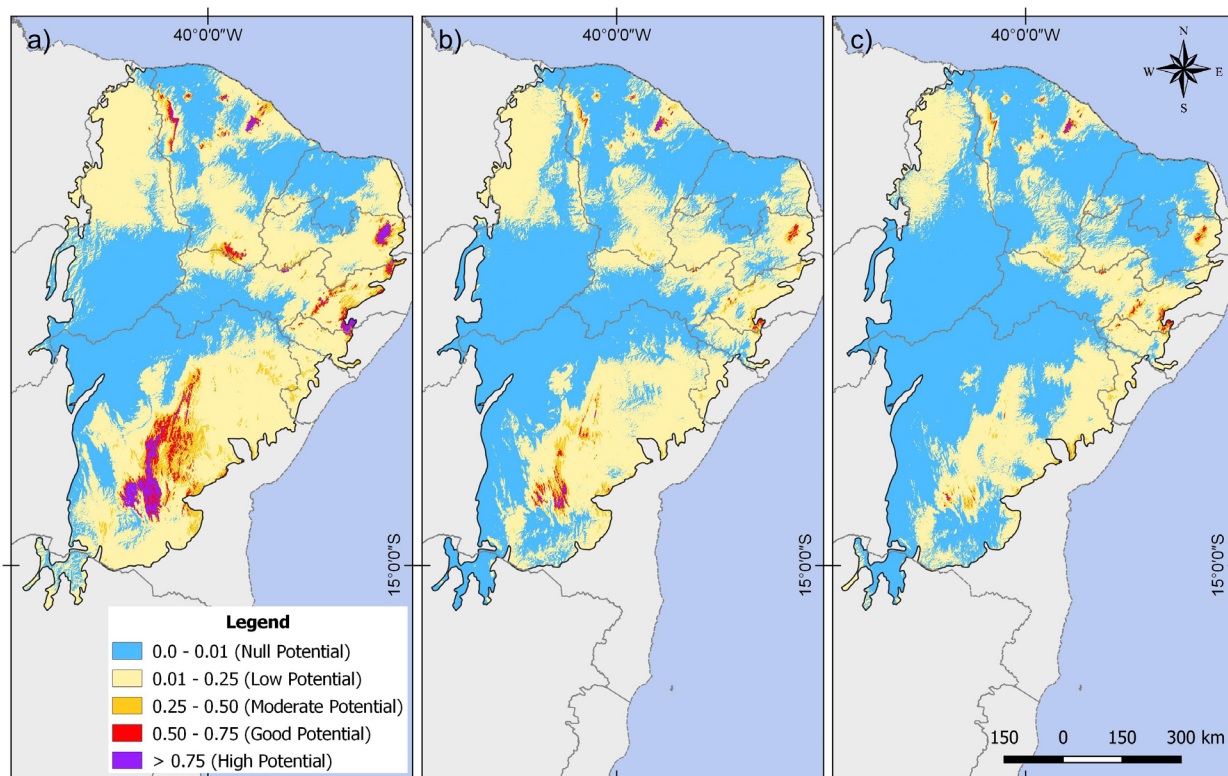
The contraction of the areas with high potential (>0.75) did not occur uniformly in the rainforest enclaves of the biome (Figure 2a) for the climate conditions and time ranges considered. Of particular note is the most pessimistic scenario (RCP8.5/2070), where only a small fraction of the enclaves in Northern Ceará state and Eastern Chapada Diamantina (state of Bahia) presented remaining areas with high potential, respectively, of 26 km<sup>2</sup> and 0.5 km<sup>2</sup> (Table IV, Figure 4c).

The remaining enclaves in Northern Ceará showed the greatest resistance, maintaining 2.4% of these areas, concentrated in the Baturité mountains. With respect to the other enclaves, Araripe Complex and Borborema Plateau, the losses of areas with high potential were total in scenario RCP8.5/2070. In the case of the Araripe Complex, total loss was also found in RCP4.5/2050 (Table IV, Figure 3b).

**Table III. Absolute and relative values of the areas with potential presence of the target species in relation to the climate status in the Caatinga biome.**

Class	Climate Condition					
		Current	RCP4.5		RCP8.5	
High Potential (> 0.75)	Interval (years)	1961-1990	2041-2060 (2050)	2061-2080 (2070)	2041-2060 (2050)	2061-2080 (2070)
	Area (km <sup>2</sup> )	10,392	1,161	349	289	27
	Variation (%)	----	-88.8	-96.6	-97.2	-99.7
Good Potential (0.50-0.75)	Interval (years)	1961-1990	2041-2060 (2050)	2061-2080 (2070)	2041-2060 (2050)	2061-2080 (2070)
	Area (km <sup>2</sup> )	15,877	3,584	2,180	1,550	308
	Variation (%)	----	-77.4	-86.3	-90.2	-98.0
Moderate Potential (0.25-0.50)	Interval (years)	1961-1990	2041-2060 (2050)	2061-2080 (2070)	2041-2060 (2050)	2061-2080 (2070)
	Area (km <sup>2</sup> )	40,329	13,993	9,335	6,225	1,775
	Variation (%)	----	-65.3	-76.8	-84.5	-95.6
Low Potential (0.01-0.25)	Interval (years)	1961-1990	2041-2060 (2050)	2061-2080 (2070)	2041-2060 (2050)	2061-2080 (2070)
	Area (km <sup>2</sup> )	440,820	363,717	290,433	243,207	217,299
	Variation (%)	----	-17.5	-34.1	-44.8	-50.7
Null Potential (0.0-0.01)	Interval (years)	1961-1990	2041-2060 (2050)	2061-2080 (2070)	2041-2060 (2050)	2061-2080 (2070)
	Area (km <sup>2</sup> )	319,056	444,037	524,182	575,228	607,105
	Variation (%)	----	+39.2	+64.3	+80.3	+90.3

Negative sign (-) means contraction and positive sign (+) expansion.



**Figure 3.** Simulation of the current potential distribution (a) and those projected for 2050 (b) and 2070 (c) under scenario RCP4.5 for epiphytic cacti in the Caatinga biome.

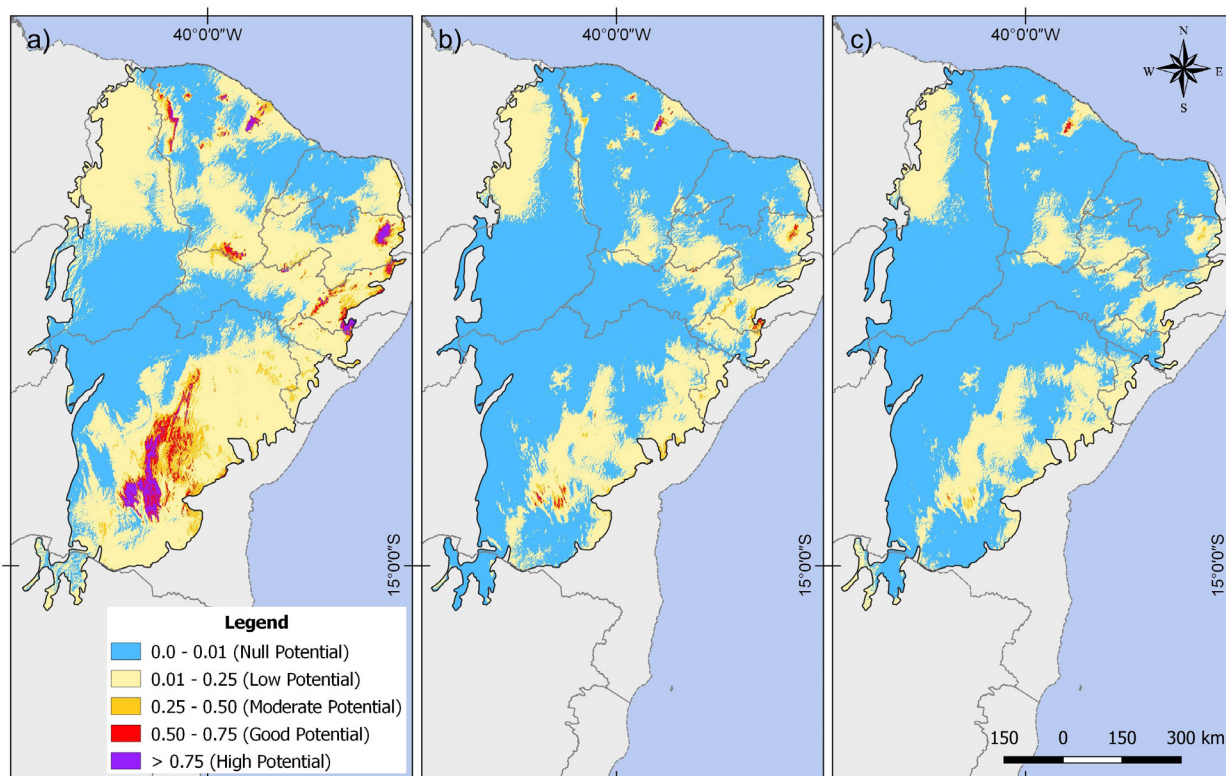
## DISCUSSION

The construction of the distribution models was strongly influenced by four of the five environmental variables (Bio5, Bio12, Bio14 and Ele). Bio12 and Bio14 together contributed 56%. This high joint contribution was expected, since these two variables are related to precipitation. Rain is the dominant climatic element controlling life in the Caatinga biome, responsible for starting and ending various ecophysiological processes, such as phenology and germination of seeds (Albuquerque et al. 2012). Furthermore, depending on the combination of volume and spatial-temporal distribution of rain in the biome, the result can be favorable or critical for the survival of young plants (Araújo et al. 2005) and the presence of species in determined places (Silva et al. 2017).

The other two variables, Bio5 and Ele, together contributed 34%. These variables also directly and indirectly have an important role in controlling various biological events in the biome, such as the distribution of species when these variables are correlated. Rising elevation is directly related to lower temperature, which reduces evaporation rates and can influence the permanence of water available to plants in specific places, thus affecting the occurrence of species (Cavalcante et al. 2000).

For the target species as well as the rainforest enclaves that sustain them, the regular supply or rain is just as important as its annual volume (Bio12). This is supported by the fact that Bio14 was the variable that most contributed to the differentiation of the areas with potential for the presence of the target species. The regular distribution of rain during the year is essential to maintain the moisture of





**Figure 4.** Simulation of the current potential distribution (a) and those projected for 2050 (b) and 2070 (c) under scenario RCP8.5 for epiphytic cacti in the Caatinga biome.

the forest enclaves. The regular supply of water depends on orographic precipitation along with dew, which complements the action of the systems causing regional rainfall, such as the ITCZ.

In this context, the distribution of epiphytic cacti in the Caatinga biome is primarily influenced by exceptional moisture conditions, and secondarily by the occurrence of tropical rainforest stands located in mountainous enclaves of the biome, which serve as support and whose occurrence also depends on exceptional moisture conditions. In those enclaves, the distribution of epiphytic cacti occurs in narrow ranges of conditions, and the classes of areas with greater potential for presence are positively related to elevation, indicating the importance of local mesoclimates.

Therefore, any expectation of alteration of the environmental conditions where epiphytic

cacti occur will point to the same prognosis for the rainforests that sustain them. This allows suggesting that the epiphytic cacti, when taken as a functional group, can act as a potential bioindicator, signaling reduction of local moisture and contraction of the rainforest enclaves in the biome.

In relation to the projections for spatial contraction observed in the areas with potential presence of the target species in the Caatinga biome (Table III, Figures 3 and 4), these are not uncommon. Other researchers have also indicated the same tendency for other plant species of the biome in the future (Rodrigues et al. 2015, Silva et al. 2019), as well as for its rainforest enclaves (Zanin et al. 2016). Furthermore, Silveira et al. (2019) demonstrated that the current rainforest enclaves of the Caatinga biome that offer support to the target species underwent major expansion during the

**Table IV. Absolute and relative values of the areas with high potential for presence of the target species in the different rainforest enclaves in relation to the climate status in the Caatinga biome.**

Enclave	Climate Condition								
	Current	RCP4.5/2050		RCP4.5/2070		RCP8.5/2050		RCP8.5/2070	
	Area (km <sup>2</sup> )	Area (km <sup>2</sup> )	Variation (%)	Area (km <sup>2</sup> )	Variation (%)	Area (km <sup>2</sup> )	Variation (%)	Area (km <sup>2</sup> )	Variation (%)
Northern Ceará	1,112	357	-67.9	272	-75.5	230	-79.3	26	-97.6
Araripe	110	0	-100	0	-100	0	-100	0	-100
Borborema	2,166	28	-98.7	25	-98.8	4	-99.8	0	-100
Diamantina	6,995	777	-88.9	51	-99.3	55	-99.2	0.5	-99.9

Negative sign (-) means contraction.

Last Glacial Maximum (21 kya) and retraction in the Middle Holocene (6 kya), since when they have remained relatively stable regarding area. What attracts attention in the present study is the projections for strong contraction in a short time frame (under 100 years) in response to the climate changes envisioned for this century, especially of the areas with good and high potential for presence (>0.50), which correspond to nearly all of the biome's rainforest enclaves.

For the areas of good and high potential presence, two future contraction scenarios were best evidenced: 1) a scenario of strong contraction, but with significant presence of remaining areas, such as the climate condition of RCP4.5/2050; and 2) a scenario of disappearance of nearly all these areas, as in RCP8.5/2070. Besides the strong contractions observed in both scenarios, they also showed in common the presence of remaining areas mainly in the extreme northern part of the biome. This finding is intriguing, since it strengthens the assumption of different impacts of climate changes in different parts of the biome.

Torres & Marengo (2014) already identified that the southern part of the biome presented medium to high values of the Regional Climate Change Index, causing them to label it as an area where the projected climate changes

would mainly involve aridization. In turn, here we identified that the northernmost part of the biome would concentrate the remaining areas with good and high potential, i.e., remaining rainforest areas, principally the enclaves in Northern Ceará. These areas would be maintained by the action of the ITCZ, the main system causing rainfall in this part of the biome, together with orographic rains and dew, decisive elements to counteract aridization. Therefore, uneven aridization could occur, more intense in the south than in the far north of the biome. This differentiated effect of climate change was also observed by Sales et al. (2015) for temperature and precipitation during this century in the region, with the Northeast region (containing the Caatinga biome) having been subdivided into northern and southern parts by those authors.

Mountainous ecosystems will certainly be affected by global warming in the 21st century, with substantial loss of biodiversity being predicted by the various species distribution models. Depending on the geographic extension, range of elevations and spatial resolution of the data used to create these models, different habitat loss rates are predicted, with associated risks of species extinction (Randin et al. 2009). The findings of Lamprecht et al. (2018), along with our investigation of the epiphytic cacti

in rainforest enclaves of the Caatinga biome, corroborate the claim of ecological and biogeographic transformations in mountainous ecosystems due to climate change.

In view of this, it is urgent to plan actions in the short, medium and long terms for adaptation of epiphytic cacti and the forests that sustain them in front of climate change. The future negative impacts on these rainforest enclaves of the Caatinga biome suggested here, both for the scenario of least impact and that of greatest impact, justify preventive adaptation actions such as making local people aware not to extract specimens from their habitats, conserve the trees etc. These actions should not only involve the target species investigated here, but also other species with similar demands (bromeliads, orchids etc.), considering all rainforest enclaves. In closing, it should be recalled that although climate change is global, the effects are always local.

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Cavalcante AMB idealized and developed this study, performed the analysis, interpreted the results and worked on the manuscript. Sampaio ACP processed the data and built the models. Duarte AS and Santos MAF contributed to the text revision.

