



# The impacts of the exposure of cactus species of the genus *Tacinga* to climate change in the Caatinga biome

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## ABSTRACT

Although some studies have investigated the effect of climate change in the Caatinga biome, Brazil, its impacts on cactus species are yet to be understood entirely. We assessed if cactus species in the Caatinga biome will benefit from or be harmed by climate change in the coming decades. We modeled the distribution of *Tacinga inamoena* and *Tacinga palmadora*, two cactus species native to seasonally dry tropical forest. We evaluated these species' range dynamics in two Shared Socioeconomic Pathways (SSP), SSP2 and SSP5, for two time periods centered in 2050 and 2070. For this purpose, we used the Maximum Entropy and Boosted Regression Trees tools to model the species distribution. The results indicated a continuous and significant contraction of the species range in the face of climate changes. We estimated that 65% of the range of *T. inamoena* and 27% of *T. palmadora* would be lost in the most critical scenario, SSP5/2070. Climate variables, such as annual precipitation and maximum temperature of warmest month, mainly drove this contraction. Results showed a high overlap in potential refugia areas with the target species. Our results can help protect refugia for cacti species, especially those of the genus *Tacinga*, throughout the Caatinga biome.

**Keywords:** Seasonally dry tropical forest, climate refugia, suitable climate area, webbed cactus species, species distribution model.

## Introduction

The general forecast for the Earth's arid and semiarid regions reflects higher average temperature, lower rainfall, and increased frequency of prolonged drought (Mirzabaev *et al.* 2022). Studies have shown that global drylands are expected to increase by the end of this century due to aridization triggered by climate change (*e.g.*, Feng & Fu 2013). Considering projections for climate alterations during the rest of this century, there is a growing demand

for studies to evaluate the effects of future climate on biodiversity, including those using models for predicting the impacts of an imminent global redistribution of species driven by climate change (Bellard *et al.* 2012). The effect of climate change on species range throughout drylands is, in general, controversial. Previous studies with cacti species project a significant loss of suitable habitat in the next decades (Albuquerque *et al.* 2018; Breslin *et al.* 2020; Pillet *et al.* 2022), especially in the Caatinga, a seasonally dry tropical forest in Brazil (Simões *et al.* 2020; Cavalcante

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& Sampaio 2022). The Caatinga is regarded as an essential part of the world's third-largest geographic center of cactus diversity (Taylor & Zappi 2004). Thus, predicting the effects of changes on species distribution in the Caatinga is one of the main concerns of conservationists since climate change influences the local persistence or extinction of species (Cavalcante *et al.* 2020a).

The cactus family (*Cactaceae*) is an important botanical family in drylands, especially Caatinga (Flora e Funga do Brasil 2020). Data from the International Union for Conservation of Nature (IUCN) indicate that 19% of the world's cactus species are endangered, and 14% are classified as vulnerable or near threatened (IUCN 2022). In Brazil, 32% of species are endangered, and 21% are vulnerable or near threatened. In the Caatinga, 31% of cacti are endangered, and 20% are vulnerable or near threatened. While Caatinga is regarded as an essential part of the world's third-largest geographic center of cactus diversity (Taylor & Zappi 2004), the impacts of the exposure of cactus species to climate change are yet to be understood entirely in this geographic space.

In this sense, an open question is whether the cactus species in the Caatinga will benefit from or be harmed by climate change in the coming decades. Some studies predicted that cactus species would expand their range (Marengo 2008) based on cacti's multiple physiological and morphological adaptations that enable them to tolerate stress in hot and dry climates (Santos *et al.* 2014). Others indicated that climate change is a potential risk for their extinction (Cavalcante & Duarte 2019; Simões *et al.* 2020; Cavalcante & Sampaio 2022).

To help elucidate this question, species distribution models (SDMs) are robust numerical tools that associate places of occurrence of species with the prevailing environmental conditions to estimate the suitability of habitats (Elith & Leathwick 2009). These models have been widely applied to forecast species' range dynamics in response to climate changes (Hijmans & Graham 2006). Knowing the geographic range and how it changes with time is fundamental to characterizing species' evolutionary history and evaluating extinction risks (Gaston 2003).

The primary goal of this study was to investigate if cactus species in the Caatinga biome will expand or contract their range in the coming decades. The objectives of this study were threefold: (1) to model the potential distribution of two flat-jointed cactus species (*Tacinga inamoena* (K.Schum.) N.P.Taylor & Stuppy and *Tacinga palmadora* (Britton & Rose) N.P.Taylor & Stuppy) in the Caatinga to assess the range dynamics during the remainder of this century in response to climate change scenarios; (2) investigate the species range dynamics, *i.e.*, to identify the main environmental variables affecting the future geographic distributions, and (3) identify the effect of the most relevant climate predictors on the contraction and expansion of the habitat and refuge of *T. inamoena* and *T. palmadora*. Investigating the impacts

of the exposure of cactus species to climate change is critical to help decision-makers conserve and protect cacti species' habitat in the Caatinga.

## Materials and methods

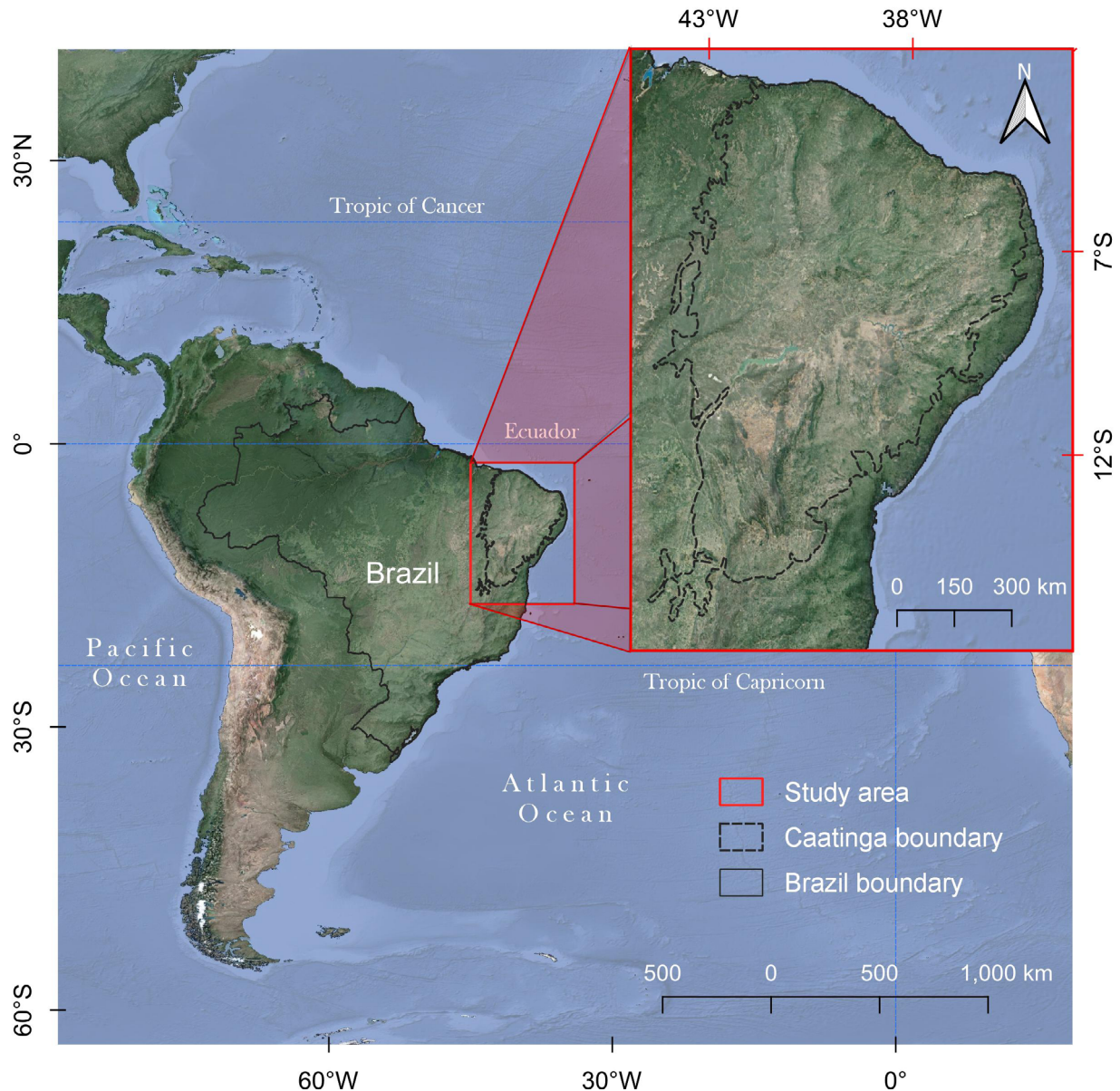
### Study area and target species

The area studied is located in eastern Brazil and covers the largest seasonally dry tropical forest in South America, known as the Caatinga (Fig. 1). It is an exclusively Brazilian forest type, mainly composed of xerophytic plant species that are subject to a semiarid climate (Andrade-Lima 1981). The average yearly temperatures vary from 25 °C to 30 °C, and annual average rainfall ranges from slightly under 400 mm to a bit above 1,200 mm. The number of dry months increases from the margins to the region's interior, with some places subject to 7 to 10 months of water deficit (Silva *et al.* 2017). The soils have a complex spatial distribution, forming a mosaic with different types ranging from shallow, stony soils supporting large cactus species to deep sandy soils mainly bearing arboreal vegetation (Velloso *et al.* 2002).

There are roughly 200 botanical families in the forest area studied, of which *Cactaceae* is among the most important, with 24 native genera, 94 species, and 40 subsp. (Flora e Funga do Brasil 2020). Of this botanical family, we initially selected six species of the genus *Tacinga* (Britton & Rose). From these, only two were finally included for having sufficient presence records for modeling: *Tacinga inamoena* and *Tacinga palmadora*. These webbed cactus species with shrubby or subshrubby habits are highly adapted to dry conditions, so they have a wide distribution in the Caatinga and endemic to Brazil (Taylor & Zappi 2004). Currently, these target species are not considered endangered (IUCN 2022). The reasons we chose species of the *Tacinga* genus were: (1) their segmented and flattened stem morphology (stem form); (2) enough records for modeling (Sampaio & Cavalcante 2023); and (3) the fact that other cacti from the Caatinga with columnar and globose form and epiphytic habits have already been modeled in previous research projects on the potential distribution of cactus in the biome in response to climate change.

### Modeling

We used the Maximum Entropy (Maxent) and Boosted Regression Trees (BRT) to describe the relationship between known places of occurrence of species and the environmental characteristics of these places. Maxent estimates the probability of maximum entropy distribution in a particular geographic space, *i.e.*, the most uniform distribution possible regarding a species, given the restrictions imposed by the predictor variables (Phillips *et al.* 2006). The BRT model involves iterative optimization that combines regression



**Figure 1.** Location of the study area (red rectangle) in eastern Brazil, the current limit of the Caatinga biome (dotted line), with an area of 844,453 km<sup>2</sup>, or 10% of Brazilian territory and 75% of the semiarid region.

trees with a boosting algorithm. It is a stepwise method where the residuals of the previous trees weighted by the learning rate are modeled in the next step, called “reinforcement”, until the interactions no longer diminish the residual deviation (Elith *et al.* 2008). The operational procedures of this study were implemented in R version 4.2.1 (R Core Team 2022). We used the functions “maxent” and “gbm.step” from the “dismo” library of R (Hijmans *et al.* 2021) to fit the Maxent and BRT models, respectively. The “Maxent” function was obtained from the Maxent version 3.4.1 software (Phillips *et al.* 2017). The scripts employed are available in the online repository “Github” (<https://github.com/AugustoPraciano/TacingasRangeDynamics.git>).

## Species data

The presence records of the target species were obtained as decimal geographic coordinates from the online database called Global Biodiversity Information Facility (GBIF 2022). We only selected points with valid coordinates collected as of 2000 (the advent of commercial GPS devices). Duplicate records and those spatially coordinated by a radius smaller than one arc minute (~ 2 km) were removed by a simple spatial rarefaction method to achieve a separation compatible with the spatial resolution of the climate data. With the cleaning process, a total of 273 (*T. inamoena*) and 132 (*T. palmadora*) high-quality records were used in



the study, overcoming the minimum required number of specimen records for the Caatinga biome according to Sampaio and Cavalcante (2023). Furthermore, we extracted 10,000 random background points (standard) throughout the study area for the Maxent models. We generated the same number of random pseudo-absence (random) points for the BRT models, collected at a minimum distance of 1 arc minute from the presence records (Breslin *et al.* 2020).

## Environmental predictors

Initially, we obtained 19 bioclimatic variables from the WorldClim 2.1 database (Fick & Hijmans 2017), representing average yearly values for the period 1970–2000 (current climate), with a spatial resolution of 30 arc seconds (~1 km). We also included altitude, derived from the digital elevation model of the Shuttle Radar Topographic Mission, and the soil data (Embrapa 2011) with the same resolution as the climate data.

We separated sets of correlated variables with a Spearman coefficient ( $\rho$ )  $\geq 0.7$ . This threshold is a good indicator of when the collinearity starts to severely distort the estimation by the model and subsequent prediction capacity (Dormann *et al.* 2013). We then applied principal component analysis (PCA) to all the variables, producing independent orthogonal axes. In each set of correlated variables, we selected the one with the highest percentage contribution to the variances for the first four PCA axes (more explanatory) and discarded the others. Therefore, starting from an initial set of 21 predictor variables, we selected eight individual variables: isothermality (Bio3); maximum temperature of warmest month (Bio5); annual precipitation (Bio12); precipitation of driest month (Bio14); precipitation seasonality (Bio15); precipitation of warmest quarter (Bio18); altitude (Alt) and soil (Sol).

## Adjustment and evaluation of the models

To avoid overfitting, the parameters applied to the models were based on the size of the species samples available according to the recommendations of Phillips and Dudík (2008) for Maxent and Elith *et al.* (2008) for BRT. The models were fitted to the datasets of current species occurrence and climate conditions. Each model resulted from an average of 20 replications, of which 25% of the presence records were separated for testing. The remaining 75% were used for training, with replacement at the end of each replication. Cross-validation was applied to assess the predictive performance of the data retained in each round.

The area under the curve (AUC) of the receiver operating characteristic was used to indicate the accuracy of the models. The AUC represents the chance that a randomly chosen presence record will have a suitability score greater than a randomly chosen absence record (Merow *et al.* 2013). To analyze the statistical significance of the AUC value, we generated 1,000 null models for each species studied,

with random samples having the same data size as the real species. We then evaluated the null models with the same retained records used to assess the models with real species. This approach corresponds to the null hypothesis that the models fitted with species records do not surpass those fitted with random samples to predict the presence of records retained for testing (Bohl *et al.* 2019).

## Transfer to future scenarios

The fitted models for the current climate were transferred to different future climate change scenarios belonging to the Hadley Global Environment Model 3 (HadGEM3-GC31-LL) of the CMIP6 (Coupled Models Intercomparison Project), obtained from WorldClim 2.1 (Fick & Hijmans 2017). We used the same predictor variables to fit the models, with a spatial resolution of 30 arc seconds. The CMIP6 variables used were Shared Socioeconomic Pathways – SSP2 (moderate scenario) and SSP5 (critical scenario) (Riahi *et al.* 2017), corresponding to the previous versions of the greenhouse gas emissions (Representative Concentration Pathways) RCP4.5 and RCP8.5. The time intervals considered were 2041–2060 and 2061–2080, respectively, centered in 2050 and 2070.

The predictions of the models returned an estimate of habitat suitability for the species, which varied from 1 (suitable) to 0 (unsuitable) (Merow *et al.* 2013). However, to estimate the size of the current range and the future changes in ranges of the target species, the continuous maps of habitat suitability were converted into presence/absence maps with the application of a threshold that maximized the sum of the specificity (currently predicted absences) with the sensitivity (correctly predicted presence records) (Liu *et al.* 2013).

The models were used to project the current SCA (suitable climate area) and to predict the range dynamics in future climate scenarios. The expanded, contracted, or refuge areas were calculated for two conditions: limited to the current distribution range of the species (without dispersion) and with unlimited dispersion. Thus, we generated two extremes of the probabilities of dispersion of the species (Benavides *et al.* 2021).

## Results

### Performance of the models

The Maxent and BRT models produced good predictive accuracy, as shown by the AUC values, and they presented equivalent results regarding the current and projected future climate scenarios. However, the BRT models had slightly higher AUC values for *T. inamoena* (0.81) and *T. palmadora* (0.90) than the corresponding values of the Maxent models (0.80 for *T. inamoena* and 0.88 for *T. palmadora*).

The actual (target) species models by both methods were significantly better in comparison with the null (random) models, with AUC values greater than 95% (95th percentile) of the null models ( $p$ -value = 0.05), thus rejecting  $H_0$ . The effect size between the AUC values of the real and null species was also large. Therefore, the AUC distributions with real species were significantly better than those with null models, indicating that the presented models were sufficiently informative.

## Influence of the predictor variables

About the relative average contributions of the predictor variables to the modeling of the distribution of the target species, the variable with the most significant contribution for both species was Bio12, with 68.6% (Maxent) and 39.0% (BRT) for *T. inamoena* and 55.0% (Maxent) and 51.3% (BRT) for *T. palmadora*. Bio5 was the second most important climate variable, contributing 5.5% (Maxent) and 8.6% (BRT) for *T. inamoena* and 12.8% (Maxent) and 11.2% (BRT) for *T. palmadora*. Other relevant variables were Soil, which contributed 9.3% (Maxent) and 18.5% (BRT) for *T. inamoena*, and the variable Bio3, with 15.4% (Maxent) and 8.8% (BRT) for *T. palmadora* (Table 1).

Bio12, the variable that most influenced the modeling of the target species by the two techniques (Maxent e BRT), was negatively correlated with forecast habitat suitability. The partial dependence plots showed the marginal responses of the habitat suitability of *T. inamoena* and *T. palmadora* to Bio12. The marginal responses for both species indicated they occur in low ranges of annual precipitation, showing that the two species have peak habitat suitability around rainfall of 500 mm a year and that yearly precipitation values above 1000 mm can be unfavorable for their occurrences (Fig. 2).

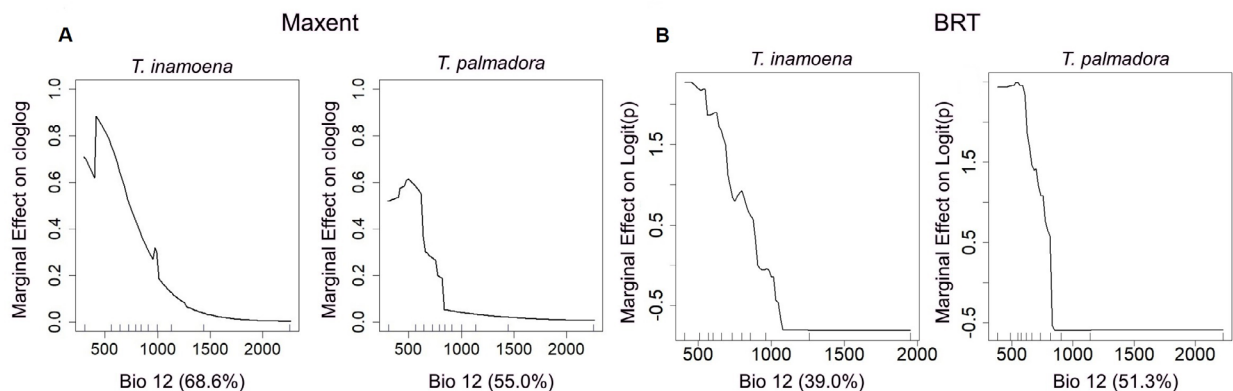
## Species range dynamics

Concerning the range of the target species in the current climate condition, both species occupy an ample portion of the area studied. The size of the range or relative area occupied by the target species in the study areas was approximately 29% (Maxent) and 32% (BRT) for *T. inamoena* and 21% (Maxent) and 22% (BRT) for *T. palmadora*. In general, the delimitation of the range areas coincided for the two species, with both being concentrated in the central part of the study area and, from there, extending along the eastern border (Figs. 3A, 3F, 4A, 4F).

**Table 1.** Relative mean contribution of the environmental variables to the SDMs.

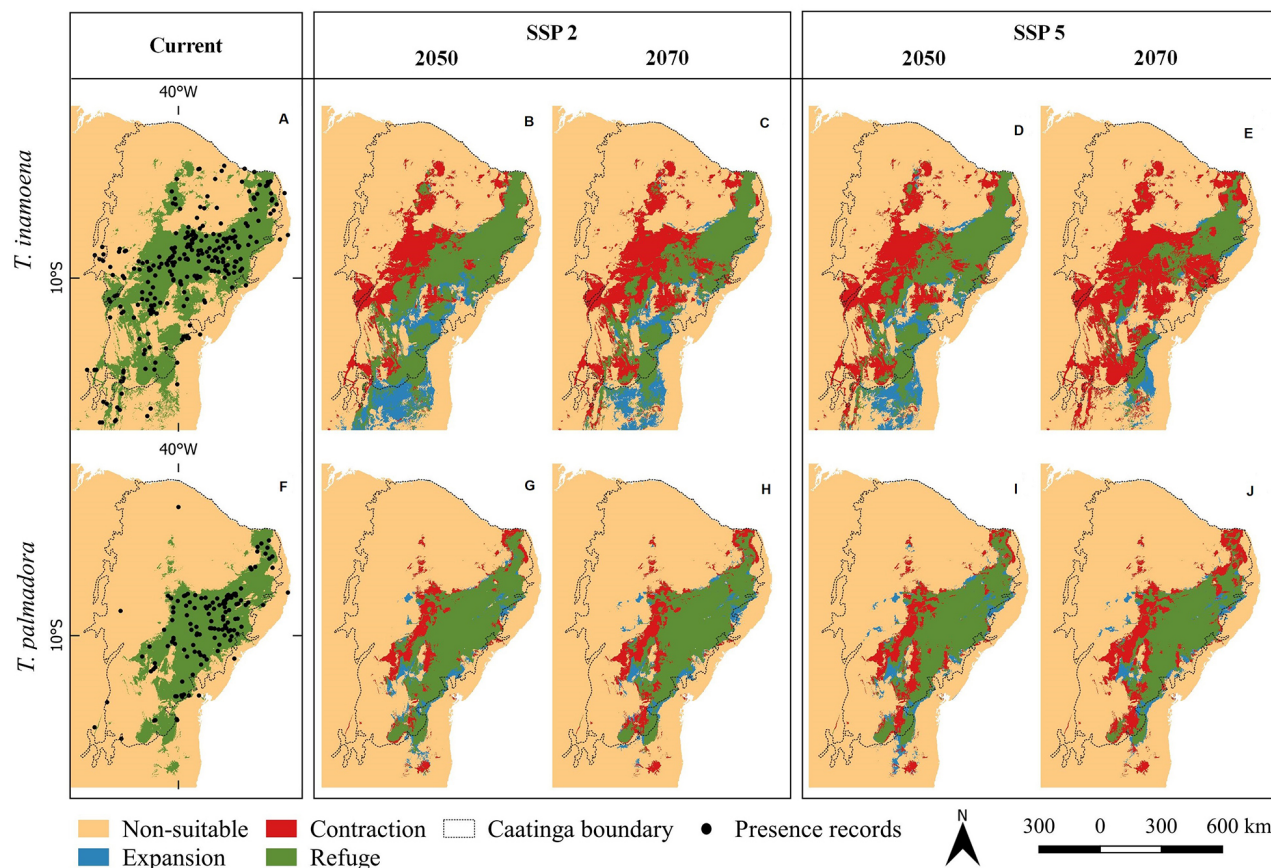
| Method | Species             | Variable Contributions (%) |      |       |       |       |       |     |      |
|--------|---------------------|----------------------------|------|-------|-------|-------|-------|-----|------|
|        |                     | Bio3                       | Bio5 | Bio12 | Bio14 | Bio15 | Bio18 | Alt | Sol  |
| Maxent | <i>T. inamoena</i>  | 1.8                        | 5.5  | 68.6  | 0.7   | 6.1   | 3.0   | 5.0 | 9.3  |
|        | <i>T. palmadora</i> | 15.4                       | 12.8 | 55.0  | 3.3   | 3.5   | 4.1   | 0.4 | 5.4  |
| BRT    | <i>T. inamoena</i>  | 6.1                        | 8.6  | 39.0  | 2.5   | 8.5   | 6.9   | 9.8 | 18.5 |
|        | <i>T. palmadora</i> | 8.8                        | 11.2 | 51.3  | 5.5   | 8.7   | 5.7   | 1.6 | 7.1  |

Species Distribution Models (SDMs); Maximum Entropy (Maxent); Boosted Regression Trees (BRT); Isothermality (Bio3); maximum temperature of warmest month (Bio5); annual precipitation (Bio12); precipitation of driest month (Bio14); precipitation seasonality (Bio15); precipitation of warmest quarter (Bio18); altitude (Alt) and soil (Sol).



**Figure 2.** Partial dependence plots showing the marginal responses of the habitat suitability of *T. inamoena* and *T. palmadora* to the variable Bio12 (annual precipitation), with the other variables held constant and considering the MAXENT (A) and BRT (B) methods. The y-axis denotes the clog log output in Maxent and the logit scale with centered values to have a mean zero of the data distribution in BRT. The x-axis represents the annual precipitation (mm). Percentages in parentheses are the contributions of the variables to the final model (Table 1). Maximum Entropy (MAXENT); Boosted Regression Trees (BRT).





**Figure 3.** Species' range dynamics according to the Maxent model under future climate change scenarios for *T. inamoena* (A-E) and *T. palmadora* (F-J) across the Caatinga. Black dots are the species' presence records. Red areas represent SCA contraction areas, blue represents SCA expansion areas, and green is refuge areas. Suitable Climate Area (SCA); Maximum Entropy (MAXENT); Shared Socioeconomic Pathways – SSP2 (moderate scenario) and SSP5 (critical scenario).

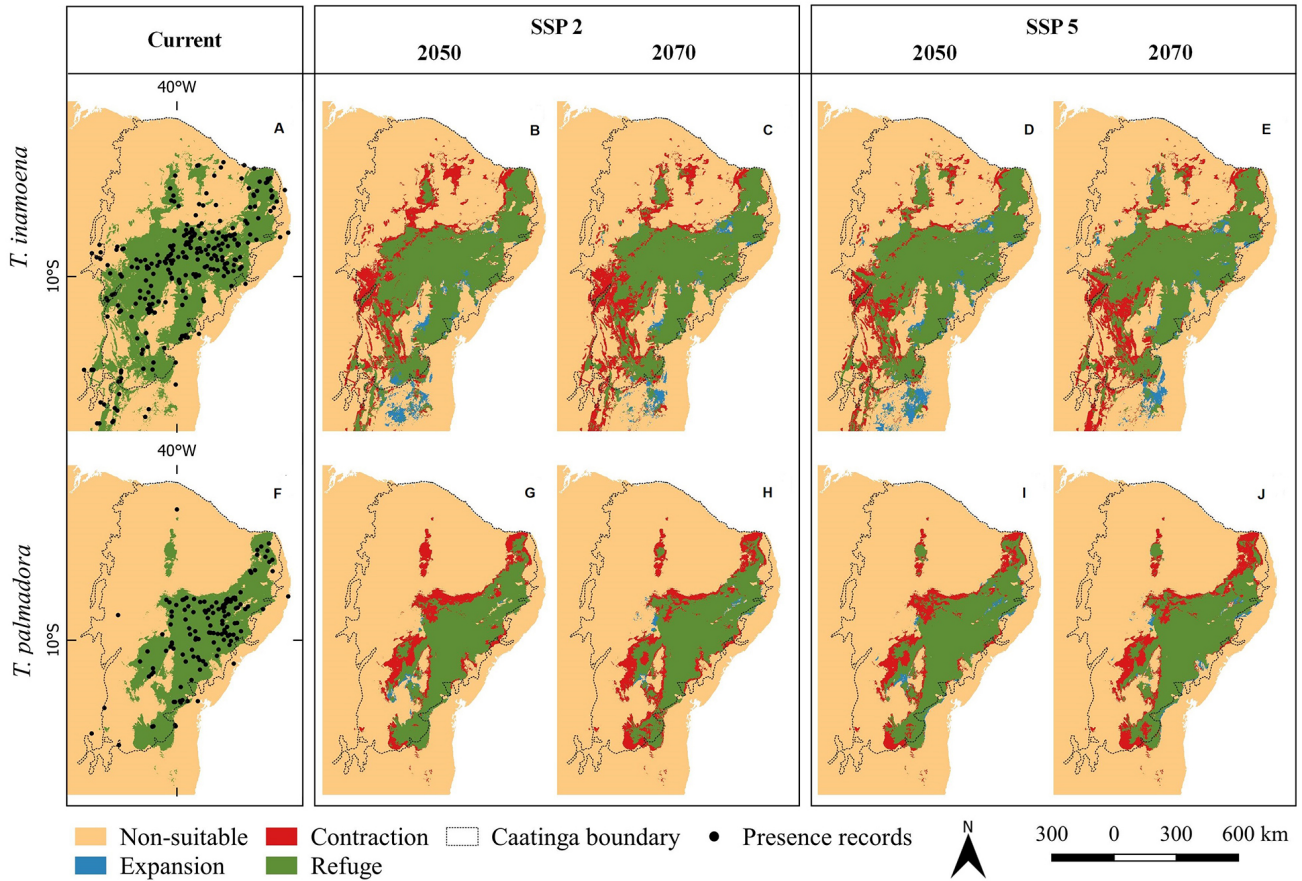
When the current models were transferred to the climate scenarios projected for the future, the new models generated mainly indicated a contraction of areas of the target species concerning the current models in all the scenarios analyzed and small expansions in some cases (Figs. 3, 4). Besides this, there were no significant differences between the extremes, considering the unlimited dispersion and absence of dispersion about the current range of the target species, indicating that the dispersion capacity is not a factor limiting the future distribution of the species. Therefore, the results described hereafter refer only to the unlimited dispersion case.

The Maxent results indicated negative impacts of climate change on the potential distribution of *T. inamoena* and *T. palmadora*. Contractions of suitable climate areas (SCA) are expected in both cases. For *T. inamoena*, a loss of 32% (SSP2) and 65% (SSP5) are expected for 2070. For *T. palmadora*, reductions of SCA of up to 15% (SSP2) and 27% (SSP5) are expected for 2070. The contraction movements of the SCA

of the target species will occur steadily in both scenarios during the remainder of the century (Table 2).

Results indicated a large concentration of SCAs (red areas) in both cases. Contractions areas are mainly located in the western part of the biome (Fig. 3). Results also show that *T. inamoena* can also be more vulnerable to fragmentation of its climatic refuge areas (green areas) in future scenarios (Figs. 3B-E). *Tacinga palmadora*, in turn, should maintain its core climate refuge area while continuing to lose area, mainly in the western and northern parts of its current range (Figs. 3G-J). Although the results for both species showed expansion of the SCA (blue areas), the prevailing movement in both cases was SCA contraction.

The BRT models' results were generally similar to those of Maxent, although with percentage values slightly smaller for *T. inamoena* and larger for *T. palmadora* (Table 2). Therefore, according to the BRT and Maxent models, the predominant movement will be a contraction of the SCA of the target species due to climate changes during the rest of this century.



**Figure 4.** Species' range dynamics according to the BRT model under future climate change scenarios for *T. inamoena* (A-E) and *T. palmadora* (F-J) across the Caatinga. Black dots are the species' presence records. Red areas represent SCA contraction areas, blue represents SCA expansion areas, and green is refuge areas. Suitable Climate Area (SCA); Boosted Regression Trees (BRT); Shared Socioeconomic Pathways – SSP2 (moderate scenario) and SSP5 (critical scenario).

**Table 2.** Absolute and relative values for the species' range dynamic with the climate state in the Caatinga considering unlimited dispersion for MAXENT and BRT models.

| Model/species       | Climate Condition       | Current   | SSP2             |                  | SSP5             |                  |
|---------------------|-------------------------|-----------|------------------|------------------|------------------|------------------|
|                     | Interval (year)         | 1971-2000 | 2041-2060 (2050) | 2061-2080 (2070) | 2041-2060 (2050) | 2061-2080 (2070) |
| MAXENT              |                         |           |                  |                  |                  |                  |
| <i>T. inamoena</i>  | Area (km <sup>2</sup> ) | 395.312   | 337.821          | 267.208          | 286.220          | 140.273          |
|                     | SCA change (%)          |           | -14.54           | -32.41           | -27.60           | -64.52           |
| <i>T. palmadora</i> | Area (km <sup>2</sup> ) | 278.751   | 246.099          | 235.740          | 233.507          | 204.686          |
|                     | SCA change (%)          |           | -11.71           | -15.43           | -16.23           | -26.57           |
| BRT                 |                         |           |                  |                  |                  |                  |
| <i>T. inamoena</i>  | Area (km <sup>2</sup> ) | 433.639   | 346.118          | 333.058          | 373.945          | 348.806          |
|                     | SCA change (%)          |           | -20.2            | -23.2            | -13.8            | -19.6            |
| <i>T. palmadora</i> | Area (km <sup>2</sup> ) | 293.250   | 217.971          | 212.646          | 227.051          | 219.618          |
|                     | SCA change (%)          |           | -25.7            | -27.5            | -22.6            | -25.1            |

Negative sign indicates contraction of Suitable Climate Area (SCA); Maximum Entropy (Maxent); Boosted Regression Trees (BRT).



For the changes in the SCA, models show a large and stable refuge area (green shading) in the central portion of the study area for *T. inamoena* (Figs. 4B-E). For *T. palmadora*, models show a continuous and stable refuge area in southeast Caatinga (Figs. 4G-J). A common potential refuge area of the target species is indicated in both cases.

Finally, the boxplots showed intervals of values for Bio5 and Bio12 in SCAs (current, contracted, expanded, and refuge), of both target species, for the most critical future climate scenario (SSP5/2070) (Fig. 5). For Bio5, the intervals for contracted or lost SCAs (boxplots with red polygons) were higher than current SCA (gray polygons), for both species and modeling methods (Figs. 5A, 5B). Results indicate that the warmest month in a hotter future scenario could promote the contraction of the SCAs of both target species. Regarding the expanded SCAs or gains (blue polygons) and refuge areas (green polygons), the intervals for Bio5 were higher than the current SCAs (gray polygons) (Figs. 5A, 5B). Results suggest that generally higher Bio5 temperatures in the future would characterize a considerable portion of the SCAs of the target species. However, their occurrences would be restrictive as of a critical threshold value.

For Bio12, the most critical aspect was the expanded SCAs (boxplots with blue polygons). Most values were above the respective intervals for the current SCAs for both species and modeling methods (Figs. 5C, 5D). This indicates that SCA expansion in the most critical future climate scenario can occur in places with higher rainfall. For the contracted SCAs (red polygons), the intervals for Bio12 were similar to current SCAs, except for *T. inamoena* in the BRT model (Fig. 5D), suggesting that changes in annual rainfall will not be directly related to the contraction of SCAs. For the areas of climate refuge (green polygons) in comparison with current SCAs, the Bio12 intervals were slightly lower, possibly indicating that even intervals with low annual precipitation will not be harmful to the persistence of the target species in the future since those species are well adapted to low rainfall.

## Discussion

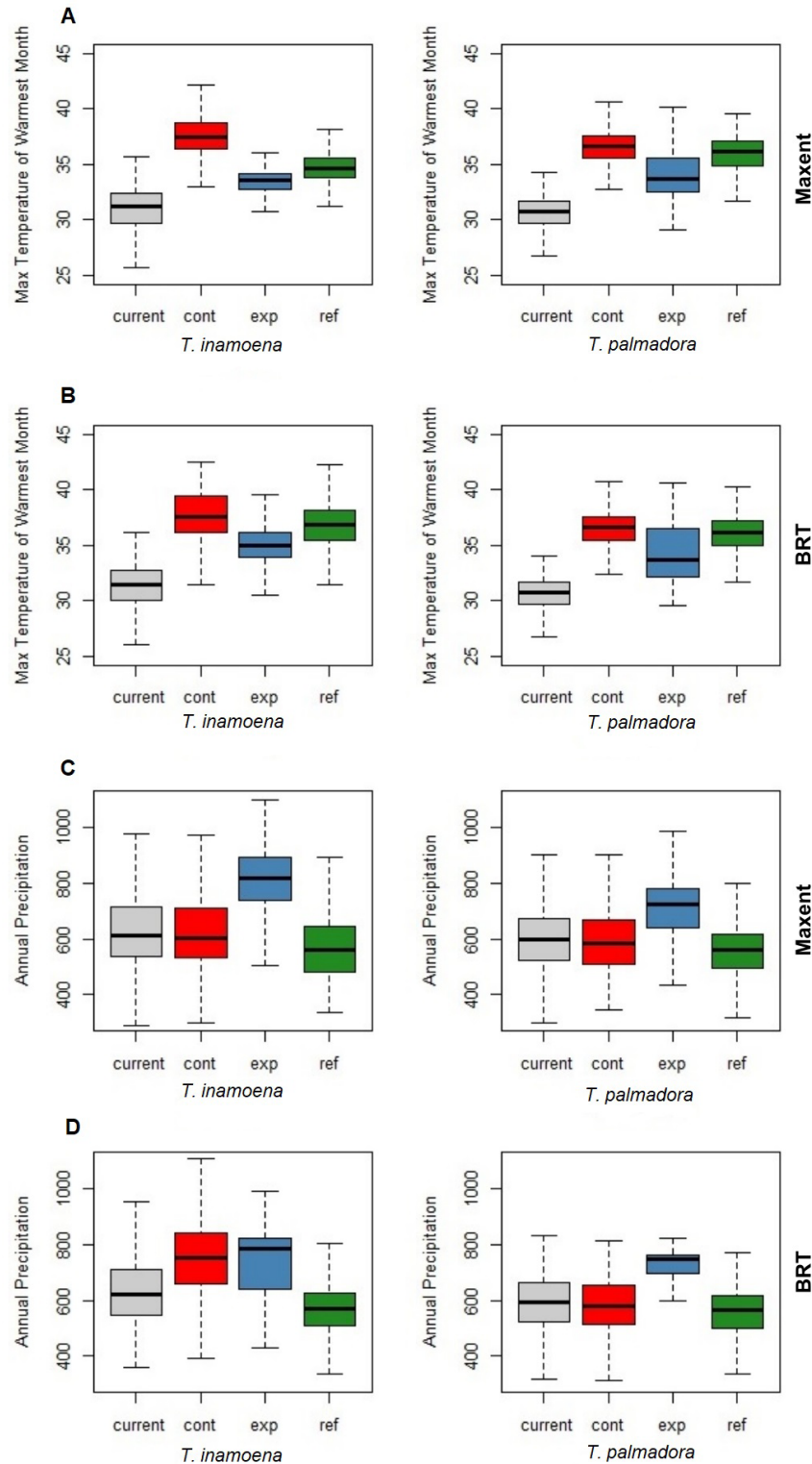
### Environmental variables

For the target species, and presumably, for the other plant species in the Caatinga, the variables indicated as exerting dominant control were related to climate, specifically rainfall, and temperature. These variables are responsible for starting and ending various biological processes, such as flowering, pollination, and seed germination, and defining species' presence or absence in a determined place in the biome (Albuquerque *et al.* 2012; Silva *et al.* 2017).

Annual precipitation (Bio12) was the climate predictor with the most substantial relative influence in modeling the target species. Although its future impact on the spatial dynamics of cactus species, in general, has yet to be made clear, due partly to the medium confidence level of the projections for the biome, our results revealed that range expansion could be associated with the areas with higher annual precipitation. Results also suggest that annual precipitation can be an important factor in buffering the losses of suitable habitats of *T. inamoena* and *T. palmadora* in response to a higher temperature.

Representing rainfall, Bio12 has been reported to contribute favorably in various distribution models of cactus species but without a significant contribution in other models. Besides the target species, Bio12 significantly influenced distribution models of the columnar cacti *Pilosocereus tuberculatus*, *Pilosocereus gounellei*, *Pilosocereus catingicola* (Cavalcante & Sampaio 2022) and *Carnegiea gigantea* (Albuquerque *et al.* 2018). In other cases, annual precipitation did not influence the distribution of other cacti species, such as the epiphytic cactus species *Epiphyllum phyllanthus* (Cavalcante *et al.* 2020a) and the columnar cactus *Cochemiea halei* (Breslin *et al.* 2020), to mention a few examples. Results indicate that the annual precipitation should receive preference in models of the distribution of other cactus species in the biome in reaction to climate changes. This suggestion is supported by the fact that the climate projections point to significant changes in the yearly volume of rainfall in the area studied for the remainder of the century. However, divergences exist regarding the total amount of this rainfall.

The maximum temperature of warmest month (Bio5) was the most influential variable in determining the spatial distribution of both cacti species. This result agrees with previous studies that also reported Bio5 as an important driver of the redistribution of cactus species in the Caatinga, such as for the epiphytic cacti *Rhipsalis floccosa*, *Rhipsalis lindbergiana* (Cavalcante & Duarte 2019) and *Epiphyllum phyllanthus* (Cavalcante *et al.* 2020a), and for the columnar cacti *Cereus jamacaru*, *Pilosocereus pachycladus*, *Pilosocereus pentaedrophorus* (Cavalcante & Sampaio 2022) and *Carnegiea gigantea*, which is endemic to the Sonora desert (Albuquerque *et al.* 2018). The importance of Bio5 relates to the increase in the average of the maximum temperature values in a representative portion of the Caatinga. The max temperature increased by 0.7 °C from 1994 to 2015 compared to the reference period 1961–1990 (Cavalcante *et al.* 2020b). Also, studies conducted in Mexico with globose cacti submitted to induced heating found increased seedling mortality (Aragón-Gastélum *et al.* 2017). Therefore, our results suggest that climate, represented by measures of water (Bio 12) and energy (Bio 5), plays a key role in determining the spatial configuration of highly suitable areas for cacti species in Brazilian seasonally dry tropical forest.



**Figure 5.** Effect of the most relevant climate predictors (Bio5 and Bio12) on the SCAs of contraction and expansion of habitat and refuge of *T. inamoena* and *T. palmadora* in the SSP5/2070 scenario according to the MAXENT (A, C) and BRT (B, D) models. The boxplots show the intervals of distribution of the values of maximum temperature of warmest month – Bio5 (°C) (A, B) and annual precipitation – Bio 12 (mm) (C, D) for the current (gray), contraction (red), expansion (blue) and climate refuge (green) SCAs under the most critical future climate condition. The colored polygons represent the second and third quartiles of each distribution (50% of the sample), and the variations in the position of the polygons concerning the vertical (Y) axis indicate the climate areas that are suitable or unsuitable for the species in the future. Outliers are omitted for greater clarity. Suitable Climate Area (SCA); Maximum Entropy (Maxent); Boosted Regression Trees (BRT); contraction (cont), expansion (exp) and climate refuge (ref).



Results also support the water-energy dynamics (O'Brien 1998; O'Brien *et al.* 2000), which predicts longitudinal gradients in plant diversity would be well predicted by water and energy variables. However, the suggestion of the preferential use of water and energy as predictors to model the distribution of cactus species in the Caatinga should be considered with caution. While Bio12 and Bio5 can strongly influence many species' SCA range, justifying their use, they may have no effect or be unimportant predictors for some species. Therefore, more studies on cacti species are required to find which water and energy variables are interesting to model each species distribution.

Concerning the last two variables, topography and soil, the literature does not contain any reports that these can undergo alteration during the rest of the century due to climate changes (Stanton *et al.* 2012) and thus influence the suitability of the target species. When observing the current and future presence records, the target species preferred shallow and stony soils with medium fertility for the soil type. These physical characteristics are found in Luvisols and Neosols, which are mainly controlled by the nature of the geological substrate (Jacomine 1996). These soil types occur mainly in two areas of the Caatinga called Northern Sertaneja Depression, and Southern Sertaneja Depression (Velloso *et al.* 2002), with extensive flatlands interspersed with isolated hills.

## Suitable climate areas and conservation

When the distribution models generated for the current climate conditions were transferred to the future climate scenarios, the new models pointed to significant SCA contractions for the target species using Maxent and BRT methods. These projections for the contraction of SCAs involving cactus species are not uncommon since they have also been observed in other arid regions, such as Mexico (Dávila *et al.* 2013) and the United States (Albuquerque *et al.* 2018), among others.

Although cacti are generally adapted to high temperatures and aridity, studies have shown that they may or may not be vulnerable to future temperature and rainfall changes (Carrillo-Angeles *et al.* 2016; Breslin *et al.* 2020; Pillet *et al.* 2022). These studies and others have revealed a two-way street for the responses of cactus species to climate changes, with some species being classified as winners (expanded range) and other losers (contracted range) (Benavides *et al.* 2021).

In the case of the target species and other Caatinga cactus species modeled (Simões *et al.* 2020; Cavalcante & Sampaio 2022), the trend has been for low tolerance to exposure to future climate changes because the majority of the species evaluated have shown contraction of SCA. This finding is particularly worrying in the case of species with small habitats, especially for specialist species such as the epiphytic cacti in the Caatinga (Cavalcante & Duarte 2019; Cavalcante *et al.* 2020a).

As generalists, the studied species have a relatively greater ability for persistence because they are adapted to a wide range of precipitation and temperature levels, which enables them to tolerate and adjust to the new climate conditions expected in the future. However, the target species are still facing a contraction of SCA due to exposure to climate change, although the negative impact should be small. This statement is based on the large amplitude of the niches of *T. inamoena* and *T. palmadora* in the Caatinga, indicated by their ability to withstand low rainfall volumes, thus minimizing the projected SCA contractions. This can also occur for other generalist cactus species in the Caatinga.

We stress that the habitat fragmentation detected by the model is another factor aggravating the negative impacts on *T. inamoena* in future climate scenarios because spatial isolation increases species' vulnerability to climate changes (Breslin *et al.* 2020; Lapola *et al.* 2020). According to the 15th Meeting of the Conference of the Parties to the United Nations Convention on Biological Diversity – CBD (2022), preserving as many species as possible is important. One of the main factors threatening species' survival is habitat fragmentation caused by human encroachment. Therefore, understanding the influence of the habitat fragmentation caused by climate changes combined with those provoked directly by human activity is crucial to minimize the negative impacts on biodiversity and maximizing species conservation. In this respect, the modeling of the distribution of the target species indicated the continuing presence of large SCAs of the two species in the area studied, with the potential for refuge.

Another relevant point was the correspondence between the distribution ranges, with restriction of the current range but with unlimited migration, suggesting that the findings of this study can be used to formulate conservation measures, even in the absence of data on migration. The persistence of the target species in their current habitats (refuge), despite the effects imposed by climate changes and without significant changes in range to other areas (expansion), is a positive finding for conserving these species.

Finally, analysis of the space-time dynamics of the SCAs involving the species of the *Tacinga* genus in future climate change simulations strengthens an important aspect of the conservation of cacti in the Caatinga biome. Even though *T. inamoena* and *T. palmadora* are amply distributed in semiarid areas, these species remain vulnerable to climate changes, particularly SCA loss, if the foreseen climate changes come to pass. Knowledge of the impacts of climate changes on species distribution needs to be complemented by ecophysiological studies (of heat and water stress) to ascertain to what extent cacti can tolerate these changes. Thus, even though the species studied are not currently threatened, the SCA loss caused by climate changes combined with anthropogenic pressures can result in the population decline of the species, consequently increasing vulnerability and risk of extinction.

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## Authors' contributions

Author Contributions: AMBC conceived the research idea. AMBC, ACPS, and FSA designed the methodology. ACPS collected the data. AMBC and ACPS performed modeling and statistical analyses. AMBC, ACPS, and FSA wrote the manuscript with significant contributions from CVR.

## Conflict of interest statement

The authors declare no conflicts of interest.

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