



Climate change impacts on the *Copernicia alba* and *Copernicia prunifera* (Arecaceae) distribution in South America

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Abstract

Climate changes are one of the main factors that affect palm trees distribution in the tropics. Among the palm trees with social, economic, and ecological relevance, we highlight the native species, *Copernicia alba* Morong ex Morong and Britton and *Copernicia prunifera* (Miller) H. E Moore. An important strategy for protecting biodiversity is to identify the climate areas that will be suitable for future habitats of the species. In this sense, we used the ecological niche models (ENMs) to predict the suitable climate areas for the potential occurrence of *C. alba* and *C. prunifera* palm trees in current and future scenarios, RCP 4.5 (optimistic) and 8.5 (pessimistic), besides to evaluate these species vulnerability facing the climate changes. Our results predicted the *C. prunifera* habitat would continue to increase over the past years. In the RCP 8.5 scenario, the climate model projected an increase of 23.88% for the *C. prunifera* population between 2050 and 2070. Also, our results can be used for the application and the establishment of commercial *C. prunifera* plantations. By contrast, the predicted habitat of *C. alba* will decrease 22.2% between 2050 and 2070, according to the RCP 8.5 scenario. For both *C. prunifera* and *C. alba* species, we observed a low percentage of the potential distribution in protected areas for future scenarios. Therefore, we suggest the creation and maintenance of extensive forestry Protected Areas (PAs) with ecological corridors and the construction of germplasm banks to manage and conserve these two important palm tree species.

Keywords Conservation · Carnauba palm · Caranda · Ecological niche models

1 Introduction

Tropical ecosystems are considered one of the greatest treasures and reservoirs of the world's biological diversity, being important sources of ecological services for human beings

(Richardson and Pennington 2016; Kissling et al. 2019). However, during the past years, tropical forests have lost approximately half of their original distribution and constantly suffer the impacts caused by climate changes (Sheffield and Wood 2008; Mendoza-González et al. 2013; Bellard et al. 2014; Faurby and Araújo 2018). According to Borges and Loyola (2020) climate change can profoundly impact biodiversity and reduce ecosystem service provisioning. It is expected that these effects will intensify once climate projections suggest an increase in the global temperature of ca. 4.8 °C, putting ecosystems, societies and the economic sectors at risk.

The palm trees (Arecaceae or Palmae), a native of the tropical forests, are considered essential for the tropic's maintenance (Johnson 2011; Eiserhardt et al. 2011; Bacon 2013; Fleming and Kress 2013). Moreover, palm trees can provide a valuable source of biogeography and evolution of the tropical forests, and the vulnerability of ecosystems facing global changes (Blach-Overgaard et al. 2015; Göldel et al. 2015; Kissling et al. 2019). The *Copernicia*

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genus stands out among the palm trees genera with ecological and socioeconomic importance, representing an essential natural reservoir for geographical distribution studies in the South American dry diagonal (Cássia-Silva et al. 2019; Freitas et al. 2019). In Brazil, this genus encompasses two species: *Copernicia alba* Morong ex Morong and Britton known as caranda and *Copernicia prunifera* (Miller) H. E Moore, popularly known as carnauba palm.

Copernicia prunifera, known as the “tree of life”, is economically significant because of the commercially important wax (carnauba wax) that covers its leaves, especially younger leaves. The wax produced from its leaves is used in cosmetics, pharmaceutical capsules, electronics, food products, polishing waxes, and coatings (Sousa et al. 2015). The production value of its wax and fibers brings in more than \$55 million per year (Santos et al. 2021). *C. alba* often forms monodominant populations known as *carandazais* in the Pantanal in Brazil. This species also occurs in the Chaco of Argentina, Paraguay and Bolivia (Lorenzi 2010). The economic relevance of *C. alba* regards its wood durability, uses in rural constructions, corrals, fences, and as an ornamental plant (Araujo and Lobo 2020).

Despite these two closely related species belonging to the same genus, they are spread in different biomes. *C. alba* predominantly occurs in the Pantanal and Chaco region, while *C. prunifera* occurs in the Caatinga and Cerrado biomes, reinforcing the idea that the distribution of palm species is strongly influenced by the climate (Blach-Overgaard et al. 2010; Peterson and Soberón 2012; Ley and Hardy 2014; Velazco et al. 2021). Despite the critical role of these palm trees in tropical ecosystems, studies of their distribution pattern in the future scenarios facing climate changes are still scarce (Göldel et al. 2015; Onstein et al. 2017). In this context, understanding the factors that determine the distribution and dynamics of palm trees diversity is a great challenge. Climate changes are one of the key factors that affect the diversity patterns of these palm trees. The future climate scenarios and their effects on the maintenance of the species is crucial for the development of successful strategies for conservation and mitigating the impact of these changes on these species’ biodiversity (Couvreur and Bake 2013; Roncal et al. 2013).

Experimental, mathematical, and empirical models have been developed to predict and to evaluate the impacts of climate changes on biodiversity (Vaz et al. 2015; Vaz and Nabout 2016). Among them, we highlight the Ecological Niche Modeling (ENM). The ENMs have been used to predict the abundance, genetic variability, spatial distribution, species extinction, and biological invasions (Rodríguez et al. 2007; Guillera-Arroita et al. 2015; Bello et al. 2020). Therefore, the ENM is one of the main approaches to predict the climate change impacts and propose strategies and priority

areas for conservation (Synes and Osborne 2011; Esser et al. 2019).

Hence, our work aims (a) to evaluate the climate niches of the *C. alba* and *C. prunifera* species; (b) to assess the *C. alba* and *C. prunifera* species vulnerability to climate changes; and (c) to identify presumable strategies for conservation of these palm trees according to the climate change impacts. We used the ENM to examine these two palm tree species' current and future (considering optimistic and pessimistic scenarios) distribution patterns in South America. Our results will help create and establish potential management strategies for conservation of these two socioeconomic important *C. alba* and *C. prunifera* palm trees.

2 Material and methods

Species description – *C. alba* and *C. prunifera* species belong to the Coryphoideae subfamily. Generally, they are solitary, rarely caespitose, with circular tree crown and no visible palm heart (Lorenzi 2010). *C. alba*, the *caranda*, can grow up to 30 m in height with an average of 17–22 cm diameter trunk. This species exhibits early successional characteristics and may tolerate fires; its fruits are edible and provide food for macaws, parrots, and fish. Flowering occurs irregularly and discontinuously at any time of the year and may overlap the fruiting periods from January to May (Araujo and Lobo 2020).

Copernicia prunifera, the carnauba palm, can be found in river valleys and in seasonally flooded areas in the semi-arid region of northeastern Brazil, where they generally form monodominant populations known as *carnaubais*. The species is highly resistant to the prolonged absence of water and permanent floods (Arruda and Calbo 2004). It can grow up to 15 m in height with an average of 15–25 cm diameter trunk. Carnauba palm has many labeliform and palmate leaves, globose cup, and long petiole with spines at the base of the leaf. The species has a mixed mating system that is preferentially allogamous (Silva et al. 2017). Fruits are likely dispersed by the sanhaçu-do-coqueiro (*Tangara palmarum*) and bats (Sousa et al. 2015; Silva et al. 2017).

Occurrence, geographic area, and environmental variables

– Two sets are necessary for the ENMs adjustment: the occurrence of species and the environmental variables. We compiled occurrence data of the two palm tree species from the following databases: GBIF (<https://www.gbif.org/>) and iNaturalist (<https://www.inaturalist.org/>) using the “occ” function of the spocc package (Chamberlain 2019); species Link (<http://splink.cria.org.br/>), NeoTropTree (<http://www.neotropree.info/>), DryFlor (<http://www.dryflor.info/>), and New York Botanical Garden (<https://www.nybg.org/>) using “BIEN_occurrence_species” function of the BIEN package

(Maitner 2018) in R (version 3.6.1, R Core Team 2019). This information was obtained in September 2019.

After the data integration, we corrected the possible taxonomic and geolocalization errors of these occurrences. For this, we used different filters: (i) taxonomic filter, considering only the species listed at Global Names Resolver (<https://resolver.globalnames.org/>), using the “gnr_resolve” function of the taxize package (Chamberlain 2019); (ii) spatial filter, considering only the coordinates that did not localize in the capitals, in the centers of the countries, states or cities, GBIF headquarters, institutions of biodiversity, ocean, urban areas, coordinates and reference systems (in the case of geographical coordinates with Datum WGS-84), with zero as value, with equal longitudinal and latitudinal coordinates, using “clean_coordinates” function of the Coordinate-Cleaner package (Zizka et al. 2019); (iii) filter of missing data lack – excluding the occurrences with no latitudinal and/or longitudinal information; and (iv) filter of spatial bias – we only filtered one occurrence for each pixel (2.5 arc-minutes or ~ 5 km) of the raster for the variables that contained environmental information, excluding closely or out of the boundary coordinates to reduce the problems of adjustment and evaluation of the models, so that this filter acts on the dimensions where the original bias of occurrence records occurred (Radosavljevic & Anderson 2014; Aiello-Lammens et al. 2015). We found 466 and 430 total occurrences for *C. alba* and *C. prunifera*, respectively. After using the filters, we found 189 and 165 occurrences remains for *C. alba* and *C. prunifera*, respectively. These data are described in detail in Table S1 and S2.

The ENMs are usually adjusted considering that only the climate variable acts in the geographical delimitation of the species (Peterson et al. 2011). At first, we used 19 bioclimatic variables (BIO01-BIO19) variables were obtained from the WorldClim v1.4 dataset (for more details, see <http://www.worldclim.org>) (Hijmans et al. 2005) (Table S3). The WorldClim dataset uses altitude, temperature, and precipitation to derive climate indices (monthly, quarterly, and annual). These indices represent trends (e.g., mean diurnal temperature range), seasonality (e.g., temperature seasonality), and extremes (e.g., maximum temperature of the warmest month) that are biologically relevant. These databases were used to estimate the niche and the distribution of both species in the current and future scenarios based on the climate change prediction: for the current (integration data between 1960 and 1990) and for the future (2050–2070). These scenarios are described in terms of Representative Concentration Pathways (RCPs), for both scenarios of CO₂ emission, RCP 4.5 (optimistic) and 8.5 (pessimistic), and for six Global Climate Models (GCMs): ACCESS1-0, CCSM4, HadGEM2-AO, IPSL-CM5A-LR, MIROC-ESM and MRI-CGCM3. These are the main GCMs used in ENM works of climate change predictions for the neotropical region,

described Assessment Report of the International Panel of Climate Change (Araújo et al. 2019; Gouveia et al. 2016). The WorldClim data raster were in the GeoTiff format, with the geographical coordinate system (“lat/lon”), Datum WGS-84 and spatial resolution of 2.5 arc-minutes (~ 5 km). These variables were appropriated for the Neotropic limit proposed by Morrone (2014) and available by Löwenberg-Neto (2014), at <https://sites.google.com/site/biochartis/>, adjusted for South America, which would be the historical limit of these species (Barve et al. 2011), using “mask” and “crop” functions of the raster package (Hijmans et al. 2016). Finally, to reduce the dimensionally and collinearity of these variables, we performed the Spearman correlation analysis with the present variables, by adopting only the variables with correlation values of ($p \geq 0.7$). According to Dormann et al (2013) correlation coefficients between predictor variables of $p > 0.7$ is an appropriate indicator for when collinearity begins to severely distort model estimation and subsequent prediction. The variables used were: BIO02 [Mean Diurnal Range (Mean of monthly (max temp—min temp))], BIO03 [Isothermality (BIO2/BIO7) (* 100)], BIO08 [Mean Temperature of Wettest Quarter], BIO15 [Precipitation Seasonality (Coefficient of Variation)], and BIO18 [Precipitation of Warmest Quarter]. The correlation found in our results is available at Table S4 and Fig. S1.

Ecological niche models (ENM) – Different mathematical algorithms can produce the niche inference of a species. Generally, these algorithms can be classified into three main groups: (i) only presence, (ii) presence and absence, and (iii) presence and background (Guisan et al. 2017). When different estimated niches are projected in the geographical space (maps), the results predict the potential distribution of one species in a different manner (Qiao et al. 2015). The combination (ensemble) of the predicted results increases the possibility of the prediction improvement, once it considers the uncertain potential distribution of the species (Guisan et al. 2017). Thereby, the ENMs were adjusted using the four following algorithms: Bioclim (Booth et al. 2014), Random Forest (Breiman 2001), Maximum Entropy (MaxEnt; Phillips et al. 2006), and Support Vector Machine (SVM; Guo et al. 2005).

To evaluate the ENMs, we used presence and pseudo-presence data (randomly sampled in all the modeling limits and with the same number of occurrence data for each species). These data were partitioned into 70% for training and 30% for tests. This partition was randomly made to reposition the sample (bootstrap) for each algorithm and for each species, being realized 10 times. For each species, 40 models were predicted for the current scenario (4 algorithms × 10 replicates) and 960 models were predicted for the future scenario (4 algorithms × 10 replicates × 2 periods × 2 scenarios × 6 GCMs). The test data (occurrence

and pseudoabsence) were used to calculate the area under the curve (AUC), based on the ROC (Receiver Operating Characteristic) curve and True Skill Statistic (TSS, Allouche et al. 2006) for the maximization of the sum of sensitivity and specificity (Liu et al. 2013), considering well-adjusted models when they had values above 0.5 (Lawson et al. 2014). The AUC considers the rate of the correct and incorrect forecast (30% of presence and pseudo absence) with several suitability thresholds. To assess the accuracy of predictive distribution models, the AUC values are generally classified in: (1) random forecast (<0.5), (2) poor forecast (0.5 to 0.7); (3) reasonable forecast (0.7 to 0.9); and (4) excellent forecast (>0.9) (Elith et al. 2006; Peterson et al. 2011).

After obtaining the models, we used the ensemble technique for each algorithm and for each GCMs, from the weighted average of the standardized values for each algorithm, using only the models of each replicate and of each algorithm with AUC values higher than 0.75. Models with values higher than their limit are considered as reasonable forecasts (Elith et al. 2006; Peterson et al. 2011). The last step was calculating the threshold values of maximization of the sum of sensitivity and specificity (Liu et al. 2013) to generate models for binary outcomes and consider higher pixels as presence (1) and minor as absence (0) potential values for each species, being 0.44 for *C. alba* and 0.35 for *C. prunifera*.

Lastly, to evaluate the climate change impacts on the species distribution, we used binary maps to identify areas potentially suitable in the present and the future. Thus, we observe: (1) Areas potentially stable, suitable in the present and the future for both periods (Stable [2050 & 2070]); (2) Areas of potential habitat gain that are not suitable in the present but will be in the future for both predicted periods (Gain [2050 & 2070]); (3) Areas of potential habitat gain that are not suitable in the present but will be in the future for at least one of the periods (Gain [2050 | 2070]); (4) Areas of potential habitat loss, which are not suitable in for both predicted periods (Loss [2050 & 2070]); (5) Areas of potential habitat loss, which are not suitable in for at least one of the periods (Loss [2050 | 2070]). We also analyzed the protected areas overlap from Protected Planet (UNEP-WCMC and IUCN 2020, [www.protectedplanet.net.](http://www.protectedplanet.net/)), filtered for the IUCN categories of protected areas (“Ia”, “Ib”, “II”, “III”, “IV”, “Not Applicable”, “Not Assigned” and “Not Reported”).

All the models were generated in the GeoTiff format, with the geographical coordinate system (“lat/lon”), Datum WGS-84 and spatial resolution of 2.5 arc minutes (~ 5 km), using R (R Core Team, 2019), “bioclim” and “maxent” functions of the *dismo* package (Hijmans et al. 2012), “randomForest” of the *randomForest* package (Liaw and Wiener 2002), and “svm” of the *e1071* package (Meyer et al. 2019). Besides, for managing the data and performing the

ensembles, we used the *sf* (Pebesma 2018), *raster* (Hijmans 2016) and *tidyverse* packages (Wickham 2019). All the maps and figures were generated by the *ggplot2* package (Wickham 2016). From the models proposed in different scenarios based on known and projected environmental parameters, we indicate strategies for conservation of two evaluated palm tree species.

The climatic niche overlap – To extrapolate the climatic niche overlap between palm tree analyzed species, we used Schoener’s model (Schoener 1970; Warren et al. 2010), as proposed by Broennimann et al. (2012). First, we reduced the environmental space, based on the 19 bioclimatic variables (only for current scenarios), using the ordination technique (PCA-env sensu Broennimann et al. 2012). The PCA-env was calibrated using the combination of the climate information of all the modeling limits. The two first PCA-env axles were gridded into 100×100 cells, covering the maximum and minimum values of the data, using the “ecospat.grid.clim.dyn” function of the ecospat package (Broennimann et al. 2018). The first and the second PCA axles captured $\sim 57\%$ and $\sim 17\%$ of the data variation, respectively, totalizing around $\sim 74\%$ of the explanation (Fig. S2). Lastly, we performed the similarity tests for the Schoener D index using the “ecospat.niche.similarity.test” function for analyzing the niche conservatism (alternative = “greater”, i.e., the niche overlap is more equivalent/similar than random) between the two studied species, with 999 bootstraps, using the ecospat package (Broennimann et al. 2018). These values range from 0 to 1; values close to 0 indicate low climatic niche overlap (niche differentiation) and values close to 1 indicate higher climatic niche overlap (niche conservatism) (Broennimann et al. 2012).

3 Results

Ecological niche models (ENMs) – The ENMs showed reliable results regarding to the evaluation values. The mean values and standard deviation of AUC were (0.96 ± 0.02) for *C. alba* and (0.92 ± 0.04) for *C. prunifera*, as well as the mean values and standard deviation of TSS were (0.83 ± 0.05) *C. alba* for and (0.76 ± 0.08) for *C. prunifera*, indicating a good prediction of model replicas. We highlight the Random Forest model as the best performance, with 0.962 for *C. alba* and 0.969 for *C. prunifera* (Table S5, Fig. S3 and S4) (Elith et al. 2006; Peterson et al. 2011). The models predicted distribution areas for both species that matched the rate distribution patterns. (Fig. 1). The generated maps revealed the Chaco, considered the central area for *C. alba* occurrence, as the most suitable region for its species, especially in Argentina, Bolivia, and Paraguay. In Brazil, the *C. alba* distribution is restricted to the Mato Grosso and Mato Grosso do Sul

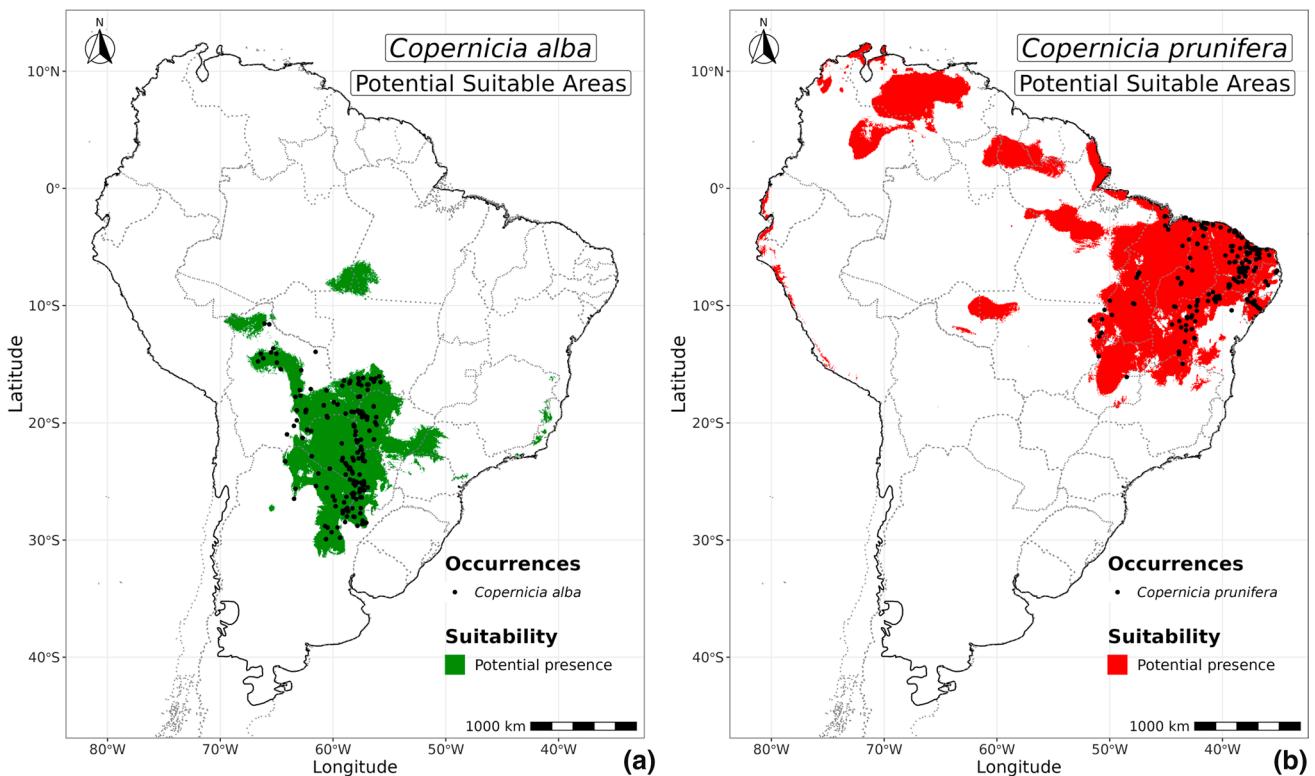


Fig. 1 Occurrences and current potential distribution of *C. alba* (a) and *C. prunifera* (b) species

States. For *C. prunifera*, the potential distribution area was the Brazilian Northeast, a dry area with high temperatures and seasonal water deficit. Therefore, the distribution in the current period can be an essential aid for the reforestation programs of the *Copernicia* species.

The climatic niche overlap – The PCA-env graphic showed the *C. alba* occurrence area has low isothermality and high-temperature seasonality, while *C. prunifera* occurrence area showed lower values regarding to the seasonality of precipitation. In all simulations, the precipitation variables were the most important to determine the potential areas for the *Copernicia* species (Fig. 2a). We observed a direct influence of the climate factors in the distribution and abundance of both species.

The climatic niche overlap values found in our work indicate low overlap ($D=0.103$) (Fig. 2b). We did not observe significant differences in the niche similarity tests of the species. The *C. alba* and *C. prunifera* similarity found was $D_{sim}=0.132$ and $p=0.12$ (Fig. 2c), and *C. prunifera* and *C. alba* similarity found was $D_{sim}=0.04$ and $p=0.35$ (Fig. 2d). Thus, the observed climatic niche overlap is less than expected and the climatic areas occupied by palm trees are divergent.

Climate change impacts for *C. alba* – We verified the climate changes would have significant impacts on the potential distribution of *C. alba*. Our results obtained by the ENMs suggest that climate changes will promote variation in the suitable total area in future scenarios and change the ideal climate conditions (Fig. 3). For *C. alba*, in both RCP 4.5 (optimistic; Fig. 3a) and RCP 8.5 (pessimistic; Fig. 3b) scenarios, it was possible to identify an area reduction in all the distribution regions, with loss more observed in the RCP 8.5 when compared to the RCP 4.5. In RCP 4.5, greenhouse gas emissions will peak in 2040 and then decrease. In the RCP 8.5, the emissions keep increasing over the XXI century (Representative Concentration Pathways–RCP; Meinshausen et al. 2011).

For both predicted periods under the RCP 4.5 emission scenario, 47.8% of the current habitat will keep suitable, while new habitats will increase by 29% (2050 & 2070) and 7.3% (2050 | 2070), the previous habitats will decrease in 11.5% (2050 & 2070) and 4.2% (2050 | 2070). The models for the RCP 8.5 scenario predict the total habit of *C. alba* will decrease 22.3% (2050 & 2070) and 13.5% (2050 | 2070); around 28.0% will keep suitable with the current weather forecast (Table 1).

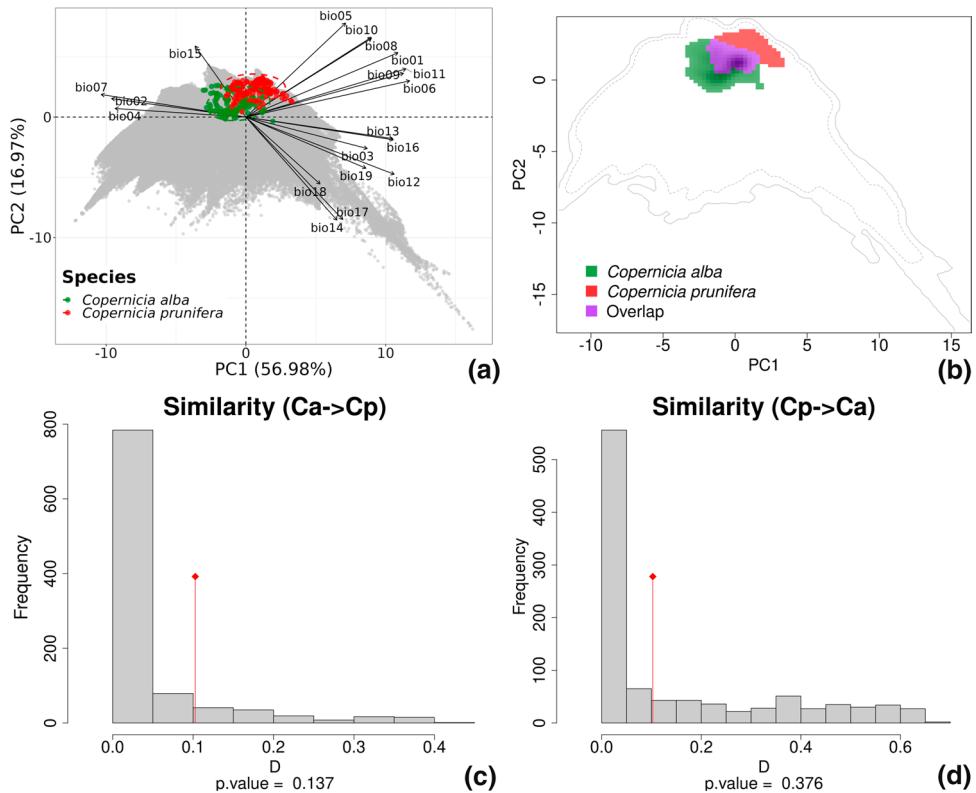


Fig. 2 Environmental niche of *C. alba* (green) and *C. prunifera* (red). **a** Biplot represents the first factorial design, which explains 73.95% of the variance. The dots represent the occurrences, and the circles encompass 95% of them. The black arrows indicate the variable direction in the first factorial design. The name of the variables follows the Bioclimatic variable patterns of Hijmans et al. (2005). **b** The niche overlap between *C. alba* and *C. prunifera* in the climate space. The green area represents the *C. alba* niche, while the red area represents the *C. prunifera* niche. The magenta area represents the overlap of *C. alba* and *C. prunifera* niches. The pixels shading represents the density in the species occurrences per cell; the solid and dotted contour lines illustrate the available environment (second design). **c, d** represent the frequency distribution of the overlapped rate of the Schoener's D niche according to the bootstrap analysis between *C. alba* and *C. prunifera*, respectively

This dynamic boosted by the climate in the boundaries will lead to changes in *C. alba* distribution. The reduction of the population distribution of *C. alba* is mainly concentrated at the central portion and Northeast of Bolivia, South of Mato Grosso, Middle East and South of Paraguay, and Northeast of Argentina. Generally, *C. alba* loses part of its current distribution climatic area but will gain few climatically suitable areas in the future. The observed pattern shows that *C. alba* will possibly suffer negative impacts from climate changes.

The models indicate that in future scenarios, the climatic suitability of this species will occur in distinct regions of its current potential distribution. The new climate changes can expose its species to warmer conditions where *C. alba* is not well adapted. According to the climatic models, the *C. alba* populations can undergo to local extinction in the borders where the climate becomes more severe. When comparing the protected areas, there is a low percentage of the potential area of protected distribution for *C. alba* in both scenarios (Fig. 3a and b). However, the optimistic scenario is better in stable areas. Gain areas have low percentages in the

protected areas compared to the total gain in 2050 & 2070, and gain in 2050 | 2070. Despite being significant, the loss concentrates out of the protected areas for loss in 2050 & 2070 and in 2050 | 2070. For the pessimistic scenario, there is a general reduction of the stable areas (Table 1).

Climate change impacts for *C. prunifera* – The Caatinga, a biome endemic to Brazil that comprehends the semi-arid region, is considered an area of climate suitability for *C. prunifera* in future climate scenarios. This climatic suitability gradually increases when compared to the current climate to 2050 until 2070 (Fig. 3c and d). Our model shows potential areas for the establishment and growth of *C. prunifera*, which significantly contributes to the local market.

In the RCP 4.5 and RCP 8.5 scenarios for *C. prunifera*, we observed growing trends with habitat availability over the years (Fig. 3c and d). The RCP 4.5 predicted 61.3% will remain as suitable habitat, while the new habitat will increase 24.7% (2050 & 2070) and 10% (2050 | 2070); the previous habitats will reduce 1.64% (2050 & 2070) and 2.3% (2050 | 2070). For the RCP 8.5, 51% of the predicted

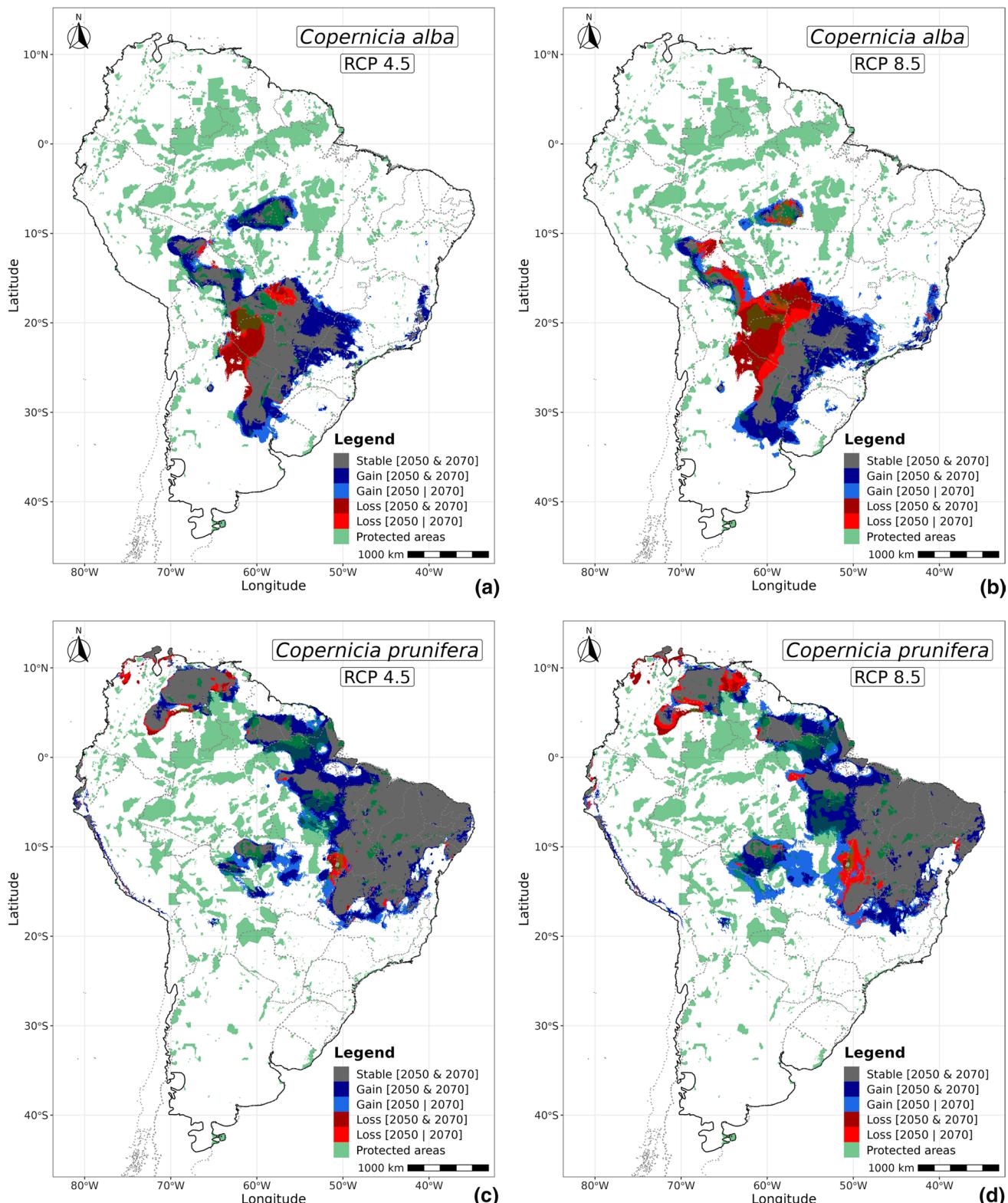


Fig. 3 Potential binary distribution of: **a** *C. alba* for the optimistic scenario (RCP 4.5); **b** *C. alba* for the pessimistic scenario (RCP 8.5); **c** *C. prunifera* for the optimistic scenario (RCP 4.5); **d** *C. prunifera* for the pessimistic scenario (RCP 8.5), between 2050 and 2070. In the maps: Stable (2050 & 2070) represents potential areas, current suitable areas that are maintained in the future; Gain (2050 & 2070) represents areas of potential habitat gain for both predicted periods; Gain (2050 | 2070) represents areas that are current suitable but will be suitable in the future 2050 or 2070; Loss (2050 & 2070) represents areas of potential habitat loss, which will be suitable for both predicted periods; Loss (2050 | 2070) current suitable areas but will not be suitable in the future 2050 or 2070

Table 1 Potential distribution of species for the optimistic (RCP 4.5) and pessimistic (RCP 8.5) scenarios, between 2050 and 2070, indicating areas of stability, gain and loss in relation to protected areas. In the Stability column: Stable (2050 & 2070) represents potential areas, current suitable areas that are maintained in the future; Gain (2050 & 2070) represents areas of potential habitat gain for both predicted periods; Gain (2050 | 2070) represents areas that are current suitable but will be suitable in the future 2050 or 2070; Loss (2050 & 2070) represents areas of potential habitat loss, which will be suitable for both predicted periods; Loss (2050 | 2070) current suitable areas but will not be suitable in the future 2050 or 2070

Species	Scenario	Stability	pa	n	per
<i>C. alba</i>	RCP 4.5	Stable [2050 & 2070]	0	47,714	40.3
<i>C. alba</i>	RCP 4.5	Stable [2050 & 2070]	1	8929	7.5
<i>C. alba</i>	RCP 4.5	Gain [2050 & 2070]	0	31,174	26.3
<i>C. alba</i>	RCP 4.5	Gain [2050 & 2070]	1	3241	2.7
<i>C. alba</i>	RCP 4.5	Gain [2050 2070]	0	8010	6.8
<i>C. alba</i>	RCP 4.5	Gain [2050 2070]	1	589	0.5
<i>C. alba</i>	RCP 4.5	Loss [2050 & 2070]	0	10,682	9
<i>C. alba</i>	RCP 4.5	Loss [2050 & 2070]	1	2920	2.5
<i>C. alba</i>	RCP 4.5	Loss [2050 2070]	0	4511	3.8
<i>C. alba</i>	RCP 4.5	Loss [2050 2070]	1	670	0.6
<i>C. alba</i>	RCP 8.5	Stable [2050 & 2070]	0	29,475	24.9
<i>C. alba</i>	RCP 8.5	Stable [2050 & 2070]	1	3728	3.1
<i>C. alba</i>	RCP 8.5	Gain [2050 & 2070]	0	30,620	25.9
<i>C. alba</i>	RCP 8.5	Gain [2050 & 2070]	1	2226	1.9
<i>C. alba</i>	RCP 8.5	Gain [2050 2070]	0	8564	7.2
<i>C. alba</i>	RCP 8.5	Gain [2050 2070]	1	1604	1.4
<i>C. alba</i>	RCP 8.5	Loss [2050 & 2070]	0	20,788	17.6
<i>C. alba</i>	RCP 8.5	Loss [2050 & 2070]	1	5510	4.7
<i>C. alba</i>	RCP 8.5	Loss [2050 2070]	0	12,644	10.7
<i>C. alba</i>	RCP 8.5	Loss [2050 2070]	1	3281	2.8
<i>C. prunifera</i>	RCP 4.5	Stable [2050 & 2070]	0	117,451	56.1
<i>C. prunifera</i>	RCP 4.5	Stable [2050 & 2070]	1	10,890	5.2
<i>C. prunifera</i>	RCP 4.5	Gain [2050 & 2070]	0	38,753	18.5
<i>C. prunifera</i>	RCP 4.5	Gain [2050 & 2070]	1	12,909	6.2
<i>C. prunifera</i>	RCP 4.5	Gain [2050 2070]	0	16,427	7.9
<i>C. prunifera</i>	RCP 4.5	Gain [2050 2070]	1	4474	2.1
<i>C. prunifera</i>	RCP 4.5	Loss [2050 & 2070]	0	2946	1.4
<i>C. prunifera</i>	RCP 4.5	Loss [2050 & 2070]	1	489	0.2
<i>C. prunifera</i>	RCP 4.5	Loss [2050 2070]	0	4069	1.9
<i>C. prunifera</i>	RCP 4.5	Loss [2050 2070]	1	776	0.4
<i>C. prunifera</i>	RCP 8.5	Stable [2050 & 2070]	0	107,054	46.4
<i>C. prunifera</i>	RCP 8.5	Stable [2050 & 2070]	1	10,533	4.6
<i>C. prunifera</i>	RCP 8.5	Gain [2050 & 2070]	0	39,993	17.3
<i>C. prunifera</i>	RCP 8.5	Gain [2050 & 2070]	1	15,066	6.5
<i>C. prunifera</i>	RCP 8.5	Gain [2050 2070]	0	32,393	14.0
<i>C. prunifera</i>	RCP 8.5	Gain [2050 2070]	1	6639	2.9
<i>C. prunifera</i>	RCP 8.5	Loss [2050 & 2070]	0	5384	2.3
<i>C. prunifera</i>	RCP 8.5	Loss [2050 & 2070]	1	498	0.2
<i>C. prunifera</i>	RCP 8.5	Loss [2050 2070]	0	12,028	5.2
<i>C. prunifera</i>	RCP 8.5	Loss [2050 2070]	1	1124	0.5

*pa: Protected área (0- outside the protected area; 1- inside the protected area); n: number of pixels of the distribution of the present in relation to the scenarios of the future (stable, gain and loss); per: percentage of the number of pixels in relation to the total number of pixels in the distribution of the present in relation to future scenarios

Table 1 (continued)

(stable, gain and loss)

climatic suitable area will remain stable. In addition, new habitats will increase 23.8% (2050 & 2070) and 26.9% (2050 | 2070) and the previous suitable habitats will decrease 2.5% (2050 & 2070) and 5.7% (2050 | 2070) (Table 1).

Until 2050, we note the emergence of new climatic suitability regions in the Middle and South of Guyana, Southwest of Suriname, and the East portion of the Rondônia Brazilian State. The model of future projection predicts that in 2070, the Northeast Brazilian region would be potentially more suitable than the current scenario. Moreover, Suriname, Guyana and French Guyana countries can become regions with high climate suitability for *C. prunifera*. These areas are considered key for *C. prunifera* preservation because they will have high climatic suitability even in the worst-case, reinforcing the idea that until 2070 there may be shifts in the geographical distribution of *C. prunifera* in South America. Most of these suitable areas are dry and water deficit regions since the annual precipitation was the variable used to predict its occurrence.

When comparing the protected areas, there is a great difference for *C. prunifera*, with a lower percentage reduction in protected areas for both climate change scenarios, despite a low percentage of the potential distribution in the protected areas (Fig. 3c and d). We observed a low percentage of stable areas in the optimistic scenario, higher for gain areas in 2050 & 2070 and 2050 | 2070. The losses are low inside and outside the protected areas for 2050 & 2070 and 2050 | 2070. For the pessimistic scenario, there general maintenance in the climatic stable areas and gain in both 2050 & 2070 and 2050 | 2070 and for the losses in 2050 & 2070 and in 2050 | 2070 (Table 1).

4 Discussion

One important strategy to protect these palm trees biodiversity is to identify suitable climate areas that will maintain propitious habitats (Borges and Loyola 2020). According to Urban (2015), the geographical distribution of the species can move under climate changes. Thus, the species must adapt, disperse, or extinguish. Modeling the potential distribution of *C. alba* and *C. prunifera* is an efficient approach to estimate the climate niche dimension and predict the potential distribution of these palm trees in South America. In this context, the high suitable regions for both species' occurrence are the best places to establish protected areas and population reintroduction.

The ENMs predicted the ongoing climate changes would threaten the *C. alba*. Especially by the exposure to climate conditions to which its species is not well adapted, representing a reduction of the climatically suitable areas that can lead to local extinction. Moreover, models predict that in both future scenarios, there will be a low percentage of the potential distribution of *C. alba* in the protected areas (Fig. 3a and b). In this sense, monitoring these populations is essential, mainly because its endemism in Chaco region.

We highlight that the rate of deforestation in the Chaco region is higher when compared to the subtropical seasonal dry forests in the world, reinforcing the urgency to develop strategies at conserving of its ecosystem (Basualdo et al. 2019). Although Chaco is considered an important socio-economic area, because of its unique diversity resulting from paleoclimate changes and vicariant events (Vallejos et al. 2015), it is not a protected area probably because of the lack of scientific knowledge. Therefore, it is urgent to develop ecological and conservational studies of the Chaco endemic and/or living species.

Moreover, the current protected areas network is ineffective (and will continue to be) to protect *C. alba* area under current and future conditions due to considerable loss of its distribution within the conservation units caused by climate change. The low protection degree and the losses caused by climate changes will lead to *C. alba* vulnerability extinction, reflecting the negligence of protecting the Pantanal and Chaco regions.

Therefore, it is necessary, to develop a systematic conservation planning for the creation and maintenance of great forest extensions of *C. alba* in protected areas, besides the designing and implementation of ecological corridors, which seek to maintain the species through time. Furthermore, palm trees conservation should be carefully planned to avoid a lack of regeneration under high grazing pressures, as these protected areas allow sustainable management and usage of natural resources (Calambáz-Trochez et al. 2021).

For *C. prunifera*, we observed an expansion of potential distribution in South America, suggesting its species adaptation to global climate changes. This increase in potential climatic distribution can reflect its species adaptation to low precipitation and drought areas globally. Besides, the climatic niche expansion for new regions can result from the adaptive plasticity of *C. prunifera* due to its occurrence in different biomes. Moreover, *C. prunifera* can adapt to disturbed environments (with vegetation removal) known as *ruderal*. It implies the species potential to develop in distinct environments, well adapting to soils with different textures and chemical composition.

The expansion of the climatic distribution of *C. prunifera* calls attention to the favorable areas for the development of commercial plantations due to the great economic and social importance of its species. The main product of exploration

and commercialization is the wax powder extracted from their leaves (Silva et al. 2017; Fajardo et al. 2018). Thereby, the climate changes can positively impact the regional productivity of *C. prunifera*, short-term improving the yield for the regions with more suitability, as the Brazilian semi-arid region. Otherwise, promoting *C. prunifera* can help raise awareness of its multiple usages and its historical and cultural significance. Additionally, incentives could increase the demand and create local markets for commercial products derived from its species. However, the *C. prunifera* cultivation in uninhabited areas should be carefully performed. Its successful application will depend on the species' adaptation to a new environment.

Although climate seasonality is a driver of palm species distribution (Eiserhardt et al. 2011), the physical and nutritional quality of the soil, together with the availability of water, also shapes plant species distribution in future scenarios (Emílio et al. 2021; Velazco et al. 2021). Therefore, studies using both climate and edaphic are also essential to generate ENMs with higher predictive power, which adds helpful information for plant distribution.

Regarding niche overlap analysis, the *C. alba* and *C. prunifera* palm trees present disjunct distribution, with low niche overlap. Moreover, previous studies indicate the historical factors related to climate and geological events can modify the habitat suitability, the establishment or persistence of species, contributing to the endemism and disjunct distribution (Hewitt 2000; Fahrig 2003; Bacon et al. 2012; Carvalho et al. 2017).

According to Jaime et al. (2015), niche conservatism occurs with sympatry species, not with species that grow in allopatry or peripatry. This pattern suggests an adaptation of new climate niches followed by the colonization of the *Copernicia* species in South America. Our results corroborate their hypothesis since we found low values of climatic niche overlap between *C. alba* and *C. prunifera*. Therefore, niche differentiation is more common than niche conservatism, indicating the taxonomic differentiation within the *Copernicia* species is related to adapting to different climates.

Allopatric speciation has probably occurred during the diversification of both species. Allopatry, the most common type of speciation, begins with the emergence of natural barriers or physical limitation that shares the geographical distribution of one species, resulting in geographic isolation, frequently stopping, or decreasing the gene flow (Benítez-Benítez et al. 2018).

As suggested by Bacon et al. (2016), when two or more taxonomic related groups are widely separated geographically, they present a high degree of climate divergence. Thus, the climate differences may have played a fundamental role in the potential distribution of *C. alba* and *C. prunifera*. These palm trees will hardly experience some ecological

interaction, as the competitive exclusion. *C. alba* shows low tolerance to dry and high-temperature environments when compared to *C. prunifera*. Consequently, the heat and dry stresses are the limiting factors that reduce the *C. alba* distribution under current and future scenarios.

Our work observed that these palm trees show different responses to climate changes in current and future scenarios. Our models clearly show a reduction in *C. alba* distribution, with higher suitability in the Chaco region. For *C. prunifera*, we observed an increase in the climatically suitable areas. For *C. prunifera*, we observed an increase in the climatically suitable areas. These areas comprehend the Tropical Dry Forests (TDFs), drastically affected by agribusiness expansion, fire forests and desertification. Climate changes can accentuate the loss of the TDFs ecosystems caused by desertification because of the dry weather and land-use practices with no adequate management (Silva et al. 2019; Lucas et al. 2021). Nevertheless, we identified a low potential distribution in the protected areas in future for both species. In this context, our maps provide a detailed comprehension of the climate change impacts over both *Copernicia* species. Our results will supply additional aids that will help the management and conservation national policies, as the creation and maintenance of the PAs and the development of in situ conservation banks, enabling the genetic conservation of *C. alba* and *C. prunifera* species.

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Data availability The authors confirm that the data supporting this study's findings are available within the article its supplementary materials. Readers interested in other/further material can request them from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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