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DIEGO CENTENO ALVARADO

INFLUENCE OF CHRONIC ANTHROPOGENIC DISTURBANCES AND CLIMATE CHANGE ON *TACINGA PALMADORA* (CACTACEAE) IN THE CAATINGA DRY FOREST: Effects on pollen traits, reproductive success and habitat suitability

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ABSTRACT

Tropical ecosystems are degrading at exceptional rates due several factors, including chronic anthropogenic disturbance (CAD) and climate change. Pollination is a key mutualistic interaction that can be affected by disturbance and climate change, due to changes in the quantity and quality of both plants and pollinators, phenological mismatches, and composition of plant and pollinator communities. Within tropical ecosystems, dry forests are considered highly vulnerable to anthropogenic disturbances and climate change due to its high population densities and human activity. The Caatinga dry forest, which harbors one of the largest and most continuous seasonally dry tropical forests, is a region characterized by its highly diversified pollination systems, however, is currently suffering high pressure from CAD and climate change. In this dissertation, I investigated how CAD and climate change influence pollen traits, reproductive success and habitat suitability of *Tacinga palmadora*, a self-compatible cactus that performs as an important food source for nectar-feeding and fruit-eating animals in the Caatinga dry forest. In the first chapter, I evaluated the effects of increasing CAD and aridity on pollen traits and female reproductive success of *T. palmadora* at Catimbau National Park. I conducted the experiments in eight plots established within the park and distributed along gradients of CAD and aridity to test for changes on pollen traits (i.e. pollen production, pollen viability, pollen-ovule ratio) and reproductive success (i.e. fruit- and seed-set). While pollen traits were negatively associated with increasing CAD and aridity, the seed-set by open pollination was positively associated with increasing CAD, while the fruit-set by open pollination was positively associated with increasing aridity. My results suggest that even though pollen traits are becoming less attractive to pollinators by increasing CAD and aridity, pollination is maintained or even increased in the most arid and disturbed areas of the park. Thus, in terms of pollination effectiveness, plant populations of *T. palmadora* might be adapted to disturbance and aridity. In the second chapter, I evaluated the effects of climate change on the range and distribution of suitable habitat for *T. palmadora* within the Caatinga dry forest. I modeled the species distribution (current and future) considering (i) usual climatic variables only and (ii) adding plant-pollinator interactions to the model. I used the CCSM4 and MIROC-ESM models for both intermediate (RCP4.5) and highest predicted (RCP8.5) GHG emission projections. Models including interaction with pollinators showed better performance and suggested that the suitable areas for *T. palmadora* will most likely be reduced in both scenarios of climate projections. Even though *T. palmadora* might be still adapted to CAD and aridity regarding its pollination, habitat suitability of the species might decrease in the future. Considering that the Caatinga dry forest is currently the least protected of all major ecoregions in Brazil, future conservation strategies are essential for the persistence and survival of this functionally-important plant species.

Keywords: Ecological Niche Modeling. Floral biology. Global change. Human disturbance. Tropical dry forest.

RESUMO

Os ecossistemas tropicais estão sendo degradados devido a vários fatores, incluindo perturbações antrópicas crônicas (PAC) e mudanças climáticas. A polinização é uma interação mutualística chave que pode ser afetada por perturbações e mudanças climáticas, devido a mudanças na quantidade e qualidade das plantas e dos polinizadores, incompatibilidades fenológicas e composição das comunidades de plantas e polinizadores. Dentro dos ecossistemas tropicais, as florestas secas são consideradas altamente vulneráveis a perturbações antrópicas e mudanças climáticas devido a sua alta densidade populacional e atividade humana. A floresta seca da Caatinga, que abriga uma das maiores e mais contínuas florestas tropicais sazonalmente secas, é uma região caracterizada por seus sistemas de polinização altamente diversificados, porém, atualmente está sofrendo altas pressões por PAC e mudanças climáticas. Nesta dissertação, investiguei como as PACs e as mudanças climáticas influenciam os traços polínicos, o sucesso reprodutivo e a adequação do habitat de *Tacinga palmadora*, um cacto autocompatível que atua como uma importante fonte de alimento para animais que se alimentam de néctar e frutas na Caatinga. No primeiro capítulo, avaliei os efeitos do aumento das PAC e da aridez nos traços polínicos e no sucesso reprodutivo feminino de *T. palmadora* no Parque Nacional do Catimbau. Conduzi os experimentos em oito parcelas estabelecidas dentro do parque e distribuídas ao longo de gradientes de PAC e aridez, para testar as mudanças nos traços polínicos (i.e. produção de pólen, viabilidade do pólen e razão pólen-óvulo) e sucesso reprodutivo (i.e. produção de frutos e sementes). Descobri que, enquanto os traços polínicos foram negativamente associados ao aumento de PAC e aridez, a produção de sementes por polinização aberta foi positivamente associada a aumento de PAC, enquanto a produção de frutos por polinização aberta foi positivamente associada ao aumento da aridez. Meus resultados sugerem que embora os traços polínicos estejam se tornando menos atraentes para os polinizadores com o aumento das PACs e da aridez, a polinização é mantida ou mesmo aumentada nas áreas mais áridas e perturbadas do parque. Assim, em termos de eficácia de polinização, as populações de plantas de *T. palmadora* podem ser adaptadas à perturbação e aridez. No segundo capítulo, avaliei os efeitos das mudanças climáticas sobre a extensão e distribuição de habitats adequados para *T. palmadora* na Caatinga. Modelei a distribuição das espécies (atual e futura) considerando (i) variáveis climáticas usuais apenas e (ii) adicionando interações planta-polinizador ao modelo. Utilizei os modelos CCSM4 e MIROC-ESM para as projeções de emissões de GEE intermediárias (RCP4.5) e mais altas (RCP8.5) previstas. Os modelos incluindo interação com polinizadores mostraram melhor desempenho e sugeriram que as áreas adequadas para *T. palmadora* provavelmente serão reduzidas em ambos os cenários de projeções climáticas. Embora *T. palmadora* possa ser atualmente adaptada a PAC e à aridez em relação à sua polinização, a adequação de habitat pode diminuir no futuro. Considerando que a floresta seca da Caatinga é atualmente a menos protegida de todas as principais ecorregiões do Brasil, estratégias de conservação futuras são essenciais para a persistência e sobrevivência desta espécie de planta funcionalmente importante.

Palavras-chave: Biologia floral. Modelagem de nicho ecológico. Mudanças globais. Perturbações humanas. Florestas tropicais secas.

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and 2099, including an optimistic (RCP4.5) and a pessimistic (RCP8.5). Solid black dots in A and D indicate locations of the sampled individuals of *T. palmadora*. Solid white triangles in D and G indicate locations of the sampled individuals of *C. lucidus*. Source of the shapes of the Brazilian and Caatinga boundaries: MMA-Ministério do Meio Ambiente, Brazil (public domain) (available for download at http://mapas.mma.gov.br/i3geo/datadownload.htm and http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm ?/caatinga/dados/shape_file/).

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SUMMARY

1 PRESENTATION

Human activities are degrading ecosystems in the tropics at an alarming rate (ARROYO-RODRÍGUEZ et al., 2017a). In addition to this, greenhouse gas emissions are the highest in history . Human disturbances and climate change can alter ranges of distribution, seasonal activities, migration patterns, interrupt biological interactions and modify abundance, structure and composition of biological species (CÂMARA et al., 2018; OLIVEIRA et al., 2017; RIBEIRO et al., 2019; RIBEIRO-NETO et al., 2016; WARREN et al., 2011).

Pollination, an important ecological interactions due to its association with the maintenance and stability of many groups of plants and animal pollinators (OLLERTON; WINFREE; TARRANT, 2011), could be negatively affected by human disturbances and climate change (AIZEN; VÁZQUEZ, 2006). Chronic anthropogenic disturbances, which are human activities that promote subtle but long-lasting removal of forest biomass (SINGH, 1998), could modify the quantity and quality of floral rewards and thus decrease plant attractiveness to pollinators (AIZEN; VÁZQUEZ, 2006; HUANG; D'ODORICO, 2020) and reduce habitat suitability for pollinators (TADEY, 2015). Likewise, climate change might modify phenological patterns, floral traits, and reduce habitat suitability for plants with specialized reproductive strategies (SCHEFFERS et al., 2016; SILVA et al., 2019a)

Tropical forests are highly vulnerable to climate change, because they host high population density and are under high human pressure (STAN; SANCHEZ-AZOFEIFA, 2019). The Caatinga, one of the largest seasonally dry tropical forests, mostly located in the Northeastern Brazil, is under high pressure from chronic anthropogenic disturbances and from climate change (QUEIROZ et al., 2017; STAN; SANCHEZ-AZOFEIFA, 2019). In this context, the objective of the dissertation is to investigate the influences of chronic anthropogenic disturbances and climate change on pollen traits, female reproductive success and habitat suitability of *Tacinga palmadora,* a self-compatible cactus with great occurrence range and that functions as an important food resource for nectar-feeding and fruit-eating animals in the Caatinga dry forest (LOCATELLI; MACHADO, 1999). Thus, I will evaluate the impacts of increasing disturbances and aridity on *T. palmadora*' pollen traits and female reproductive success (Chapter 1) and the impacts of climate change on *T. palmadora*' habitat suitability (Chapter 2).

2 THEORETICAL BACKGROUND

2.1 CHRONIC ANTHROPOGENIC DISTURBANCES

Disturbances are all those actions that somehow affect the stability of an ecosystem, which may be due to the climate, such as hurricanes or droughts, or due to biotic factors, such as pathogens or human actions (ALBUQUERQUE et al., 2018). Tropical ecosystems are being influenced by human disturbances, turning landscapes into heterogeneous matrices with different land uses (CHAZDON, 2003; GARDNER et al., 2009). In 2011, it was reported that forest degradation in the tropics accounted for 500-600 million hectares, which represents 30-40% of the total forest area in the region (BLASER et al., 2011). The loss of forest area in the tropics has been large, with reports of the greatest losses in Brazil, Indonesia and Nigeria in recent years (KEENAN et al., 2015). As these activities intensify, including over-harvesting, agriculture, cattle ranching, hunting, road construction, and mining, high rates of deforestation and degradation might occur, directly or indirectly affecting the biodiversity of these ecosystems (CHAZDON et al., 2009; GARDNER et al., 2009). If this scenario continues or escalates, the tropics are most likely to be the epicenter of current and future extinctions, and the provision of important ecosystem services would probably be reduced, as the tropics hold two-thirds of the world's biodiversity (GARDNER et al., 2009).

Human disturbances could be acute or chronic (SINGH, 1998). Acute disturbances are those that cause a large biomass removal in the short term or induce fragmentation without reducing the area, while chronic ones are those that cause a low biomass removal but continue over time (ALBUQUERQUE et al., 2018; RITO et al., 2017; SINGH, 1998) Chronic anthropogenic disturbances (hereafter referred to as CAD) could lead to the extinction of species and modification of vegetation structure, such as wood extraction and overgrazing (RIBEIRO et al., 2015). By their nature, CAD are measured on a gradient, from pristine to severely degraded sites and can be measured in different ways: (1) through biotic indicators, for example index of biotic integrity, that reflect the implications of human disturbances on biodiversity; (2) human indicators, for example human land use and proximity to towns or roads (MARTORELL; PETERS, 2005). Chronic anthropogenic disturbances can negatively affect plant and animal community structure and composition, modify plant reproductive strategies, and disrupt plant-animal interactions (MARTORELL et al., 2015; OLIVEIRA et al., 2017; RIBEIRO et al., 2015, 2019; RIBEIRO-NETO et al., 2016). The resilience of an ecosystem to chronic anthropogenic disturbances depends on the intensity of its modification, those well-preserved and biodiversity-rich native forests will persist better than those with higher human pressures (ARROYO-RODRÍGUEZ et al., 2017b).

Tropical dry forests are the most vulnerable tropical forests as they support dense and low-income human populations that contribute to the removal of biomass by collecting firewood, livestock grazing and exploitation of non-timber forest products (ARNAN et al., 2018; CÂMARA et al., 2018). Currently, only 44% of the dry forests remain because most of the area has been converted for various human uses (PORTILLO-QUINTERO; SÁNCHEZ-AZOFEIFA, 2010).

2.2 CLIMATE CHANGE

Climate change has intensified in recent years due to human activities (TRENBERTH, 2018), resulting from high levels of greenhouse gases (hereafter referred to as GHG) emissions (IPCC, 2014). The GHG emissions have had consequences in several ecological processes, such as warming of the atmosphere and ocean, reduction of snow and ice, and rise of the sea level (IPCC, 2014). These changes have several negative impacts on various ecosystems (IPCC, 2014). It is characterized mainly by global increases in temperature and divergent changes in rainfall levels, which are most likely to become more variable and extreme, resulting in increasing extreme aridity in some areas, for instance (OVERPECK; UDALL, 2020).

In the tropics, changes in the mean temperature, and frequency and quantity of precipitation, have caused increases in the frequency of extreme events, including droughts and wildfires (DEB et al., 2018). These changes might modify vegetation structure, species distribution, flowering and fruiting phenology of several species (DEB et al., 2018). In addition, it has been shown that climatic parameters, such as precipitation, might mediate the effects of chronic anthropogenic disturbances on tropical ecosystems (GIBB et al., 2015; RITO et al., 2017). Climate change can cause modifications in geographic ranges, as suitable areas are most likely to be modified, by the increase or reduction in sizes or shifts in latitude and elevation, and this changes are believed to increase extinction risk and affect biological interactions (IPCC, 2014; WARREN et al., 2011). Extinction risk may increase as the climatic envelope might change and so the optimal conditions in which the populations of a species persists (THOMAS et al., 2004). Biological interactions may be modified as shifts in geographical ranges might influence direction, frequency and intensity of interactions (BLOIS et al., 2013) .

Dry forests are defined by the seasonality in the distribution of precipitation, resulting in a long dry season (MILES et al., 2006). Likewise, these forests present physiognomies and characteristics adapted to the temperature levels and precipitation of the mentioned (MILES et al., 2006). Furthermore, even though they are thought to be harsh environments to harbor species, their endemism levels in most regions are considered to be higher than in some moist ecosystems (PORTILLO-QUINTERO et al., 2015). However, scenarios for the future predict that rainfall levels are most likely to decrease in the area by the end of the century (IPCC, 2014), probably causing several impacts on it. In tropical dry forests, the predictions indicate that precipitation levels will decrease, which may vary according to the region, since in some places a reduction of 15% is expected, while in others of 50% (STAN; SANCHEZ-AZOFEIFA, 2019). This will most likely increase aridity and cause recurrent drought events (IPCC, 2014). These ecosystems are highly vulnerable to climate change, since they host high population density and a large part of the area is being transformed for human activities (STAN; SANCHEZ-AZOFEIFA, 2019).

2.3 REPRODUCTION OF FLOWERING PLANTS

The evolution and diversification of flowering plants have experienced various changes, both climatic and from disturbances (AIZEN; VÁZQUEZ, 2006). Pollination is considered one of the most important mutualistic interactions due to its relationship with processes of maintenance and stability of ecosystems and approximately 90% of flowering plants are pollinated by animals (OLLERTON; WINFREE; TARRANT, 2011). Nevertheless, the intensity of current anthropogenic disturbances exceeds those previously experienced by the same and the functioning and performance of pollination may be threatened (AIZEN; VÁZQUEZ, 2006). The most common human disturbances which are capable of disrupting plant-pollinator interactions are fragmentation, logging, invasive species, and pollution (AIZEN; VÁZQUEZ, 2006). It has been showed that the reproduction of flowering plants could be negatively affected by chronic anthropogenic disturbances, resulting in lower quality and quantity of pollen and nectar production, reduced sizes in floral structures, less fruit- and seed set and modify plant-pollinator interactions, since the frequency of visitors could decrease (AIZEN; FEINSINGER, 1994; STEFFAN-DEWENTER; TSCHARNTKE, 1999).

Chronic anthropogenic disturbances can induce plants to reduce the quantity and quality of floral rewards, such as pollen and nectar production and pollen viability, due to allocation of resources destined for reproduction to other processes, and thus reduce plant attractiveness to pollinators (AIZEN; VÁZQUEZ, 2006; DESCAMPS et al., 2018; FANG et al., 2010; HUANG; D'ODORICO, 2020; QUESADA; BOLLMAN; STEPHENSON, 1995; WASER; PRICE, 2016). Furthermore, changes in plant density and structure due to CAD, could modify the foraging routes of pollinators (DUMINIL et al., 2016; GHAZOUL; MCLEISH, 2001) and reduce habitat suitability for pollinators (TADEY, 2015).

The main effect of climate change on plants is shifting in the phenology (start or end time, duration), which leads to a breakdown between plant and pollinator, which can also affect the reproduction, growth and dispersal of plants (MENZEL et al., 2020; PIAO et al., 2019; SU et al., 2013). High temperatures and low precipitation can detriment gamete development, affecting fertilization and post-fertilization events, such as fruit and seed formation (SILVA et al., 2020; YOUNG; WILEN; BONHAM-SMITH, 2004). These events are most likely to affect floral rewards, which in turn will also limit visitation by pollinators(HUANG; D'ODORICO, 2020). In a situation where pollination of self-compatible plants by biotic vectors is limited, selection favors self-pollination (FAUSTO; ECKHART; GEBER, 2001), which reduces the genetic diversity of the species and may affect the persistence in the community (RICHARDS, 1997). Little is known about the effects of chronic anthropogenic disturbances and climate change acting on the reproductive success of tropical dry forest plants.

2.4 THE CAATINGA DRY FOREST

The Caatinga dry forest, one of the largest and most continuous seasonally dry tropical forest (SDTF) in America, is the fourth largest ecosystem in Brazil (SILVA et al., 2018). It covers about 912,529 km² of the Brazilian territory, approximately 10,7% of the country (SILVA et al., 2018). It occurs almost exclusively in the northeastern region of the country, including the states of Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia and the northeastern part of the state of Minas Gerais (this one in southeastern Brazil) (SILVA et al., 2018). The warm semi-arid climate is marked by low levels of precipitation (most of the region receives between 600 and 1000 mm of rain a year) with rains distributed irregularly spatially and temporarily for 3 to 5 months of the year. The average annual temperature ranges between 25º and 30° C (SILVA et al., 2018). Most of the Caatinga dry forest receives between 600 and 1000 mm of rain per year, while 0.6% of the Caatinga receives less than 400 mm and 1.6% receives more than 1200 mm (DE ANDRADE et al., 2017) and its principal source is the Inter-Tropical Convergence Zone (ITCZ), which results in changes in the frequency of rainfall in space and time, increasing the occurrence of seasonal droughts in the region (RITO et al., 2017; SALGADO et al., 2015). The Caatinga dry forest is the most diversified ecosystem amongst all SDTFs in the world (SILVA et al., 2020) with approximately 3000 species, with 23% of them being endemic to the area (QUEIROZ et al., 2017). Due to the rainfall scarcity and irregularity, most of the vegetation is deciduous the proportion of endemic species is relatively high (299 species) in contrast to other SDTFs (MACHADO et al., 2017; “Reflora,” [s.d.]; SILVA et al., 2018). Although the area is influenced and limited by climatic parameters, it has few generalist flowers and diversified pollination systems, that can be compared to regions that present higher rainfall (MACHADO et al., 2017).

The Caatinga it’s one of the most populous semi-arid regions in the world, with 23 million people (equivalent to 12% of the Brazilian population), who are constantly extracting firewood from native vegetation (10 million cubic meters per year), overgrazing livestock (herds can exceed 16 million individuals) and implementing slash-and-burn agriculture (RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016). Furthermore, the future scenarios proposed by Intergovernmental Panel on Climate Change, predict that the country will suffer reduction in rainfall of 22% (IPCC, 2014), that could aggravate the effects of CAD in the biodiversity of the Caatinga (CÂMARA et al., 2018; RITO et al., 2017).

The reproduction of most flowering plants in the Caatinga depends on biotic vectors (LEAL et al., 2018; MACHADO; LOPES, 2004; MACHADO; LOPES; SAZIMA, 2006), however, anthropogenic disturbances and climate change could modify plant reproductive strategies and reduce suitable habitat for endemic plants with specialized reproductive strategies (SILVA et al., 2020, 2019b). Also, environmental changes are most likely to reduce the distribution of several endemic species due to less suitable environments(SILVA et al., 2019b). CAD and climate change are most likely to disrupt plant-pollinator interactions, an important parameter for the functioning of plant communities, and therefore reduce the persistence of the several species in the region (SILVA et al., 2020).

2.5 THE CACTACEAE, ITS POLLINATION AND REPRODUCTIVE ECOLOGY

The Cactaceae is a monophyletic family distinguished morphologically by the absence of leaves and the presence of thorns, flowers with numerous stamens and tepals, and individuals that are succulent (DE MENEZES; TAYLOR; LOIOLA, 2013). Physiologically, the family is tolerant to water scarcity, characterized mainly by the reduction of lateral branches in areoles and the stems are adapted to perform photosynthetic actions due to the absence of leaves (DE MENEZES; TAYLOR; LOIOLA, 2013). The family is endemic to the Americas, with approximately 120 genera and more than 1600 species, distributed from Canada to the Patagonia region (GOMES; ARAÚJO, 2015; PINHEIRO; FERREIRA, 2015). Brazil is considered the third-largest diversity center of the Cactaceae (TAYLOR; ZAPPI, 2004), with more species in tropical dry forests (ARIAS-MEDELLÍN; FLORES-PALACIOS; MARTÍNEZ-GARZA, 2014), as it presents approximately 260 species, occurring in all phytogeographic domains; specifically the Caatinga has 60 cacti species, 58 native and two naturalized (“Reflora,” [s.d.]).

The majority of flowers in the Cactaceae family are hermaphrodite, with few exceptions of some species considered dioecious, having separate female and male plants within its populations (MANDUJANO et al., 2010). Mating systems in the family can be classified as predominantly outcrossing, predominantly selfing, and mixed self and outcrossing (MANDUJANO et al., 2010). Cacti flowers are considered animal-pollinated and also specialized in animal pollination, including pollination by bats, birds, and insects, such as bees, wasps, moths, and ants (MANDUJANO et al., 2010). In the Caatinga dry forest, the most frequent pollination syndromes in Cactaceae species are bat pollination (LEAL et al., 2018; LOCATELLI; MACHADO; MEDEIROS, 1997; ROCHA; MACHADO; ZAPPI, 2007) and hummingbird pollination (GOMES; QUIRINO; ARAUJO, 2014; GOMES; QUIRINO; MACHADO, 2014; LEAL; LOPES; MACHADO, 2006; LEAL et al., 2018; LOCATELLI; MACHADO, 1999).

On one hand, some cacti species are considered vulnerable to disturbances due to its low individual growth rate and recruitment and also because many of those specie are endemic to extremely small area, so if those areas are converted or fragmented, the species would most likely become extinct (MARTORELL et al., 2015). Furthermore, some species can be vulnerable to climate change as biodiversity erosion might occur, disrupting important biological interactions for the species (CAVALCANTE; DUARTE; OMETTO, 2020). On the other hand, other species could tolerate human disturbances as they remain unexploited due to its thorns, that make them underutilized and neglected, and let them grow naturally in harsh environments (RANJAN et al., 2016). Furthermore, some species might be tolerant to climate changes, as they might present tolerance to water-deficit and high temperatures and light intensities (RANJAN et al., 2016).

Cacti are important food sources as their rapid growth due to the high water use efficiency produces forage for animals and fruits with edible and medicinal uses for human consumption (SHETTY; RANA; PREETHAM, 2012). Furthermore, in tropical dry forests cacti represent important food resources for several animal species during the dry season, when resources are limited (LOCATELLI; MACHADO, 1999). For the reasons described before and their vulnerability to various threats, they must be a priority for conservation (MARTORELL et al., 2015).

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4 CHAPTER 1 – MANUSCRIPT TO BE SUBMITTED TO THE JOURNAL FOREST ECOLOGY AND MANAGEMENT

Increasing chronic anthropogenic disturbance and aridity differentially impact pollen traits and female reproductive success of *Tacinga palmadora* (Cactaceae) in a Caatinga dry forest

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Highlights

- *Tacinga palmadora* pollen traits are negatively related to increasing aridity.
- Pollen traits are negatively related to increasing disturbance.
- Seed-set by open pollination is positively related to increasing disturbance.
- Fruit-set by open pollination is positively related to increasing aridity.
- Pollination efficacy of *T. palmadora* may be adapted to disturbance and aridity.

Graphical abstract

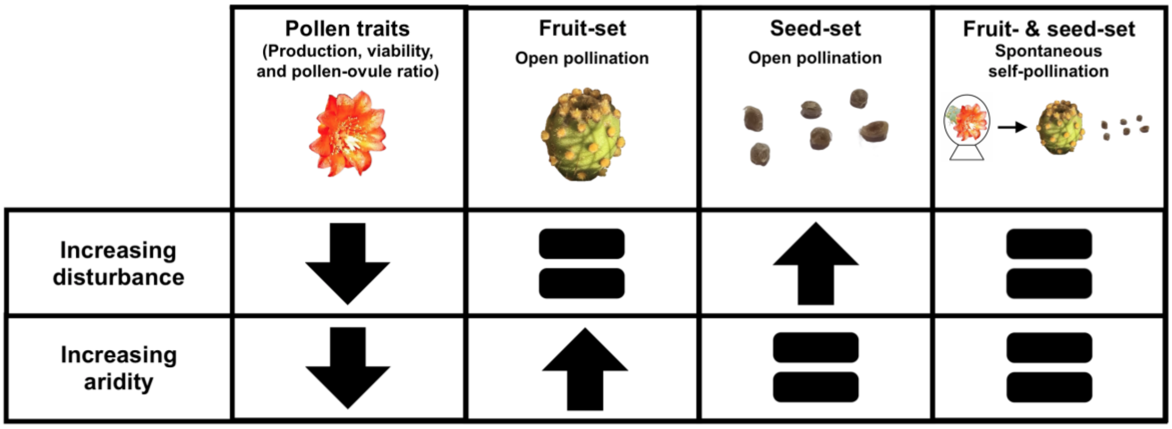

Fig. 1. Graphical Abstract

Abstract

Ecological interactions in tropical ecosystems are being modified by chronic anthropogenic disturbances (CAD) and climate change. Pollination is a key mutualistic interaction that can be affected by disturbance and climate change due to alterations in the composition, diversity and distribution of plants, floral resources and pollinators. We experimentally tested if increasing CAD and aridity induce changes in pollen traits and female reproductive success of *Tacinga palmadora*, a self-compatible cactus that performs as an important food source for nectar-feeding and fruit-eating animals, in the Caatinga dry forest. The study was carried out in eight plots at the Catimbau National Park, northeastern Brazil. At each plot we quantified disturbance and aridity intensity to be used as predictor variables against pollen traits (total pollen production, pollen viability, and pollen-ovule ratio) and female reproductive success (fruit- and seed-set by both open and spontaneous self-pollination) in generalized linear models. All pollen traits were negatively associated with increasing CAD and aridity intensity, while the seed- and fruit-set by open pollination were positively associated with increasing CAD and aridity, respectively. Spontaneous self-pollination was not influenced by increasing CAD and aridity. Our results revealed that even though pollen traits decrease with higher CAD and aridity, pollination of *T. palmadora* is maintained or even increased in the most arid and disturbed areas of the park. We conclude that, in terms of pollination effectiveness, plant populations of *T. palmadora* might be adapted to disturbance and aridity in Caatinga dry forest.

Keywords: floral biology, human disturbance, ornithophily, plant-pollinator interaction, tropical dry forest

1. Introduction

Tropical ecosystems are being modified mainly by human disturbances for both traditional and commercial purposes, including agriculture, cattle grazing, hunting, extractive forestry, mining, and the expansion of cities (Chazdon et al., 2009). Disturbances can become chronic when human activities cause subtle but long-lasting removal of forest biomass and thus alter the environment (e.g. wood extraction and overgrazing) (Singh, 1998; Ribeiro et al., 2015; Lugo, 2020). Chronic anthropogenic disturbance (hereafter, CAD) can negatively impact plant and animal community structure and composition (e.g. Ribeiro-Neto et al., 2016; Oliveira et al., 2017; Ribeiro et al., 2019), modify the diversity of plant reproductive strategies (e.g. Silva et al., 2020), and disrupt ecological interactions (e.g. Câmara et al., 2018). In addition, climate change can also play a key role in modifying ecosystem composition and structure (Deb et al., 2018). Precipitation might increase in some regions, while in others it might reduce significantly and consequently induce severe droughts (Cowles et al., 2018). Droughts can increase soil temperature and reduce humidity, thus decreasing plant productivity and diversity (Cowles et al., 2018). The consequences of climate change may also be associated with reductions of suitable habitat for endemic plants with specialized reproductive strategies (e.g. Silva et al., 2019). This might promote the disruption of many key ecological interactions (Scheffers et al., 2016).

Pollination, one of the most important ecological mutualistic interactions, is associated with the maintenance and stability of many groups of plants and animals (e.g. Ollerton et al., 2011). Globally, it is estimated that 87.5% of flowering plant species are pollinated by animals (Ollerton et al., 2011). However, pollination can be affected by anthropogenic disturbance and climatic change due to changes in the composition of the partners (both plants and pollinators) (e.g. Aguilar & Galetto, 2004; Young et al., 2004; Tadey, 2015; Phillips et al., 2018; Huang & D’Odorico, 2020). Additionally, anthropogenic disturbance may induce plants to reduce the quantity and quality of floral rewards and thus reduce plant attractiveness to pollinators (Huang & D’Odorico, 2020) and/or may reduce habitat suitability for pollinators (Tadey, 2015). On the other hand, reduced water availability in the environment (e.g. drought) can cause the reallocation of resources from plant reproductive structures to the conservation of root biomass (Phillips et al., 2018). These changes will decrease the quantity and quality of floral resources and reduce plant reproductive success (from the development of gametes to fertilization and post-fertilization events) (Young et al., 2004; Phillips et al., 2018). Pollinator activity could also be delayed or inhibited with low water availability or droughts (Ramírez & Kallarackal, 2018).

Although there are plants that can ensure the production of fruits and seeds with the lack of pollinators (i.e. plants with self-spontaneous pollination) in the face of disturbances (e.g. Ortíz et al., 2010; Chen et al., 2016) and/or climate change (e.g. Devoto et al., 2009; Maron et al., 2014; Gibson-Forty et al., 2020), pollinators are essential to avoid inbreeding and therefore, potential reduction of population genetic variability (Morales & Galetto, 2003; Blambert et al., 2016). In environments with harsh or hostile conditions, reproductive fitness by outcrossing can be limited by the shortage of pollinator visits (Ai et al., 2013). Thus, some plant traits can be favored to increase self-fertilization within the same flower. This could be recorded in arctic, alpine and arid environments, although they rarely predominate (Richards, 1997). In addition, fruit production in self-compatible plants can increase significantly with the contribution of pollinators (Morales & Galetto, 2003). All this taken together, might imply strong consequences for plant-pollinator interactions and the contribution of pollinators to the plant species reproductive success might be reduced with disturbances and climate change, thus compromising the persistence of plant populations and communities.

Within tropical ecosystems, dry forests are considered highly vulnerable because the regions they occupy host high population densities and thus most areas are converted to agriculture and livestock lands, and climate change forecasts predict that the levels of precipitation will most likely reduce (IPCC, 2014; Stan & Sánchez-Azofeifa, 2019). Caatinga, one of the largest and most diversified seasonally dry tropical forests in the world, located in northeastern Brazil (Queiroz et al., 2017), currently face several anthropogenic pressures, including cattle ranching and wood extraction (Rito et al., 2017; Arnan et al., 2018). Furthermore, the region is characterized by extreme drought due to its low water availability, with low annual precipitation levels (average annual rainfall of 773mm, of which approximately 70% falls in a single month) (Andrade et al., 2017). Despite this, its pollination systems are highly diversified, with few generalist plant species (Silva et al., 2020), resembling regions with much higher precipitation levels (Machado & Lopes, 2004). However, modifications in the environment due to increased CAD and reductions in precipitation levels will probably affect plant-pollinator interactions, influencing ecosystem functioning (e.g. reproduction) and ultimately the persistence of species in the Caatinga dry forest (Silva et al., 2020).

One of the most diverse families in the Caatinga dry forest is the Cactaceae (Queiroz et al., 2017), with most of the species being pollinated by bats (e.g. Locatelli et al., 1997; Rocha et al., 2007; Leal et al., 2017) and hummingbirds (e.g. Locatelli & Machado, 1999; Leal et al., 2006; Gomes et al., 2014a & b; Leal et al., 2017). The Cactaceae is one of the most-threatened flowering-plant families, as they are highly vulnerable to disturbances due to their low growth rate and recruitment, and because many are endemic to extremely small areas (e.g. Martorell et al., 2014). In contrast, cacti can be tolerant to arid conditions as they have mechanisms that allow them to store appreciable amounts of water for growth and tissue development (Nefzaoui et al., 2014), and some species can be even more abundant in driest areas (Ferreira et al., 2016).

In this study, we investigated the effects of increasing CAD and aridity on pollen traits and female reproductive success of *Tacinga palmadora* (Britton & Rose) N.P.Taylor & Stuppy (Cactaceae), an endemic and self-compatible cactus that is an important food resource for nectar-feeding and fruit-eating animals (Locatelli &

Machado, 1999; Lima et al., 2019; Lima-Nascimento et al., 2019), in the Caatinga dry forest. We tested the hypothesis that increases in CAD will influence pollen traits and sexual reproductive success of *T. palmadora,* as CAD might compromise species resources and interactions with pollinators. On the other hand, increased aridity will not influence pollen traits because species high tolerance to arid conditions, however, it will influence reproductive success, since it can compromise interactions with pollinators. We particularly made the following predictions:

1. increasing CAD will negatively affect *T. palmadora* pollen traits, while increasing aridity will have no influence on them;
2. isolated increasing CAD and aridity will negatively affect the female reproductive success from open pollination (with pollinators) of *T. palmadora*;
3. isolated increasing CAD and aridity will positively affect the female reproductive success due to spontaneous self-pollination (without pollinators) in *T. palmadora*.

2. Materials and Methods

2.1. Study site

This study was carried out in Catimbau National Park (8º24’00’’ to 8º36’35’’ S, 37º09’30’’ to 37º14’40’’ W) (Fig. 2), a protected area of approximately 62,300 ha in the state of Pernambuco (northeastern Brazil). The park is considered a representative portion of the Caatinga dry forest as it presents the entire precipitation variation observed in this phytogeographical domain (480 to 1100 mm) (Machado et al., 2017). The most representative plant families in the park are the Leguminosae and the Euphorbiaceae (Rito et al., 2017). In terms of reproductive traits, the park has high species richness of hermaphrodite flowers with self-incompatible mating systems, and species bearing bee-pollinated flowers are the most representative (Silva et al., 2020). The park is home for several rural and indigenous communities, whose subsistence is dependent on extensive livestock husbandry, extraction of firewood and non-timber products, and hunting (Rito et al., 2017, Arnan et al., 2018).

2.2. Study species

Tacinga palmadora (Fig. 3) is a self-compatible shrubby cactus ca. 1.5 m high (Locatelli & Machado, 1999). The species is endemic to the Caatinga dry forest (Lima et al., 2019). Flowers are hermaphrodite and last up to seven days from June to November (Locatelli & Machado, 1999). They are tubular-shaped 30-40 mm long, with red perianth and green hypanthium (Locatelli & Machado, 1999), individually displayed (1-292 flowers per plant) (Lima et al., 2019).

In contrast to most Caatinga dry forest flowering plants, *T. palmadora* flowers represent an important food source for nectar-feeding animals inhabiting the region during the dry season (Locatelli & Machado, 1999; Lima et al., 2019). Although it is a self-compatible (reproduction via both self-pollen and pollen from other individuals) and self-spontaneous (mechanical autogamy) species (Machado et al., 2006), with a ratio of self-pollination vs. cross-pollination of 1/2, flowers have a contrasting coloration with the deciduous vegetation and high concentrations of sugar in the nectar (Locatelli & Machado, 1999). The latest traits are important to attract pollinators, mainly hummingbirds, which increases the chances of cross-pollination and supports population genetic variability (Locatelli & Machado, 1999). Indeed, the species is ornithophilous, with *Chlorostilbon lucidus* (Shaw, 1812) (Trochilidae) as the main effective pollinator in areas of Caatinga dry forest (Locatelli & Machado, 1999). The species *C. lucidus* has a year-round permanence, since the vegetation of the region offers different food resources throughout the year (Machado, 2009).

2.3. Characterization of CAD and aridity gradients

We sought individuals of *Tacinga palmadora* in 20 plots of 1000 m^2 each (50 m x 20 m) along the Catimbau National Park from the ILTER (International Long-Term Ecological Research) project. We found the species in eight plots where our focal individuals (N = 5-10) were sampled (Rito et al., 2017). These plots followed wide CAD and precipitation gradients (Fig. 2).

To determine CAD values at each plot, we used a global multi-metric CAD index, applied to the Catimbau National Park, and proposed by Arnan et al. (2018). This index combines three distinct disturbance pressure measurements, here based on the main sources of disturbance in the study areas:

1. livestock pressure: sum of goat usage and cattle dung frequency (based on trail length and dung counts at field);
2. wood extraction: live wood extraction and fire-wood collection (based on field measurements);
3. people pressure: geographic distances and demographic information (based on the indirect information from distance from houses and number of people); (for further details, see Arnan et al., 2018).

For each plot, each single disturbance pressure index was estimated (with values ranging from 0 to 100, being the latter the strongest intensity) according with the following formula adapted by Arnan et al. (2018):

$$I = \left[\left(\sum_{i=1}^{n}(y_i - y_{min})/(y_{max} - y_{min})\right)/(n)\right] \times 100$$

where *I* is the overall pressure index; y_i is the observed value for one disturbance metric for the evaluated plot; y_{min} is the minimum observed value for the disturbance metric within all plots; y_{max} is the maximum observed value for the disturbance metric within all plots; *n* is the number of the individual disturbance metrics considered. To determine the global multi-metric CAD index, all the single disturbance pressure indices were thus integrated using the same formula (*sensu* Arnan et al., 2018). Disturbance intensity for the sampled plots ranged from 0 to 58.1 (Fig. 2), representing the entire CAD range observed in the park limits (*sensu* Arnan et al., 2018).

Aridity was determined as the ratio of mean annual precipitation to potential evapotranspiration (Armas et al., 2011). To determine the values of aridity at each plot, we first extracted the value of mean annual precipitation from the WorldClim global climate database from the 2005 version (Fick & Hijmans, 2017), at 30-seconds spatial resolution at the equator, with the “maptools” package version 1.0-2 (Bivand & Lewin-Koh, 2020) for R (R Development Core Team, 2019). Precipitation from the sampled plots ranged from 940 to 552 mm, representing approximately the entire range of mean annual precipitation of the Caatinga (Fig. 2) (Machado et al., 2017). We also extracted the value of a global aridity index from the CGIAR-CSI's Global Aridity and PET database using 30-seconds resolution maps (Trabucco & Zomer, 2018). Aridity index from the sampled plots ranged from 0.3 to 0.6. Afterwards, we performed correlations between the global aridity index and mean annual precipitation, and since they were highly correlated ($r = 0.97$, $p < 0.01$), we used precipitation as the measure of aridity. We also performed correlations between the CAD and aridity gradients, and since they were not significantly correlated ($r = 0.13$, $p = 0.75$), they were considered statistically independent.

2.4 Pollen traits: Total pollen production, pollen viability, and pollen-ovule ratio

We collected pre-anthesis flower buds from 80 individuals, 10 at each plot (*N* = 2-5 per individual). These flower buds were fixed in alcohol 70% (w/v) for posterior analysis. To calculate pollen production per flower, we took ten anthers from each pre-anthesis flower bud and placed each one on a slide with distilled water, opened them with needles and released all the pollen grains (Kannely, 2005). We counted the total number of pollen grains under a light microscope. Total pollen production per flower was calculated by multiplying the mean number of pollen grains per anther by the total number of anthers in each sampled pre-anthesis flower bud. To determine pollen viability of *T. palmadora*, we estimated the mean percentage of pollen grains that presented cytoplasmic content under the exposure of 2% acetic carmine (Radford et al., 1974) of ten anthers per flower. To estimate the pollen-ovule ratio of each flower bud, we divided the total pollen production by the number of ovules (Cruden, 1977), which were counted under a stereo microscope. Estimates and counting on the total pollen production, pollen viability and pollen-ovule ratio were based on ~30 pre-anthesis flower buds per sampled plot, totalizing 240 flower buds in all plots.

2.5. Female reproductive success in open (flowers exposed to pollinators) and spontaneous self-pollination (bagged flowers, without access to pollinators)

We performed two field experiments to characterize female reproductive success by measuring fruit- and seed-set under both open pollination and spontaneous self-pollination. In each plot, we tagged 30 pre-anthesis flower buds per experiment (3-6 flower buds per individual). First, we characterized reproductive success under open pollination, i.e. when pollinators are present. We marked pre-anthesis flower buds and left them exposed to floral visitors. Second, we characterized reproductive success under spontaneous self-pollination using the same individuals than in the previous experiment. We marked and bagged pre-anthesis flower buds, excluding floral visitors, by using synthetic polypropylene fiber bags. After nine weeks, we followed fruit and seed formation in all plots for each experiment. Fruit-set was determined as the proportion of fruits produced from the total tagged flowers per plot, while seed-set was determined as the number of seeds per fruit.

2.6. Statistical analyses

To test effects of CAD and precipitation on the several reproductive parameters of *Tacinga palmadora*, we carried out generalized linear models (GLMs) and generalized linear mixed models (GLMMs). For fruit-set, both under open and spontaneous self-pollination, we used GLMs where the replicates were plots. For pollen traits and seed-set, both under open and spontaneous self-pollination, we used GLMMs where the replicates were flowers or fruits and individuals nested within plots were added as random effects. For pollen production, pollen-ovule ratio, and seed-set by both open and spontaneous self-pollination, we used a Gaussian error distribution. For the fruit-set, by both open and spontaneous self-pollination, we used a binomial error distribution (fruits formed vs. not formed). For the pollen viability, we used a Poisson error distribution. We used the packages *stats* version 3.6.2 and *lme4* version 1.1-7 (Bates et al., 2020) to build the GLM and GLMM models, respectively, in R. We applied Akaike's information criterion with a small sample correction (AICc) to select the best-supported models as it is recommended for small sample sizes, multiple tests and variable collinearity (Burnham & Anderson, 2002). We based selection of models on AICc differences (ΔAICc) lower than two (Burnham & Anderson, 2002) and we considered predictors within those models the most important if they did not contain the model that only contains the intercept. For the model selection we used the “dredge” function in the *MuMIn* package (Burnham & Anderson, 2002) in R.

3. Results

3.1. Pollen traits: Total pollen production, pollen viability, and pollen-ovule ratio

Flowers of *Tacinga palmadora* produced from 792 to 79,155 pollen grains with a viability between 59.8% and 99.5%; pollen-ovule ratio ranged from 19.3 to 2,059.6 (Appendix, Table 2). As we predicted, model selection procedure indicated that all pollen traits of *T. palmadora* decreased with increasing CAD (Table 1, Figs. 4A, C & E). On the other hand, different to what we expected, model selection procedure indicated that all pollen traits decreased with increasing aridity (Table 1, Figs. 4B, D & F).

3.2. Female reproductive success in open (flowers exposed to pollinators) and spontaneous self-pollination (bagged flowers, without access to pollinators)

The fruit-set of *T. palmadora* ranged from 6.7% to 86.7%, after open pollination (i.e., with pollinators), and from 3.3% to 10%, after spontaneous self-pollination (i.e., lacking pollinators) (Appendix, Table 3). The seed-set by open pollination ranged from one to 47, and from one to 36 in the spontaneous self-pollination experiment (Appendix, Table 4). Different from what we predicted, the model selection procedure indicated that increasing CAD enhanced the seed-set by open pollination (Table 1, Figs. 4H), while increasing aridity enhanced the fruit-set by open pollination (Table 1, Figs. 4G). Increasing CAD had no influence on the fruit-set by both open and spontaneous self-pollination and on the seed-set by spontaneous self-pollination. Furthermore, increasing aridity had no influence on the fruit-set by spontaneous self-pollination and on the seed-set by both open and spontaneous self-pollination.

4. Discussion

Our results showed that increasing chronic anthropogenic disturbances (CAD) and aridity differentially impact pollen traits and female reproductive success of *T. palmadora*, so that only some of our predictions were corroborated. Regards pollen traits, both increasing disturbance and aridity reduced pollen production, pollen viability and pollen-ovule ratio. Meanwhile, reproductive success when pollinators are present was positively associated with increasing CAD and aridity.

The mean values of the pollen traits we observed in Catimbau National Park, were similar to the usual values reported in other studies (Locatelli & Machado, 1999). Interestingly, these values showed relevant spatial variability across the park. Our first prediction, that increasing CAD would reduce the values of pollen traits of *T. palmadora* but that aridity would not influence them, was partly accomplished. As regards disturbance, no livewood collection of the species has been recorded and only few direct uses by people in an ornamental way has been recorded in the region (Lucena et al., 2015; Machado et al., 2018). Nevertheless, in the Caatinga dry forest, the species contributes to approximately 40% of goat’s daily intake due to the amount of protein and energy that they provide to them (Fuentes-Rodríguez et al., 1997; Araujo et al., 2010). This kind of herbivory pressure from goat usage can thus reduce plant's photosynthetic capacity; consequently, plant individuals might reallocate the resources destined for reproduction (e.g. pollen production and viability) to defense (Quesada et al., 1995; Aizen & Vásquez, 2006) and/or to regrowth for damaged tissues reconstitution (e.g. Moreira et al., 2011). Regarding the aridity gradient, the reduction in the values of pollen traits by increased levels of aridity might be due to harsher environmental conditions. Even though, cacti species are thought to be tolerant to aridity regarding its growth and development (Nefzaoui et al., 2014), the recovery of some cacti species is strongly dependent on precipitation (López-García et al., 2001). Several studies have demonstrated that water deficit during floral development have detrimental impacts on pollen traits, reducing quality and quantity of floral rewards, including pollen production, pollen viability, and nectar (Barnabás et al., 2008; Fang et al., 2010; Waser & Price, 2016; Descamps et al., 2018). Lower pollen production and viability could decrease the capacity of seed germination (Fang et al., 2010; Waser & Price, 2016). Otherwise, with lower pollen-ovule ratio, the species will tend to receive more self-pollination (Cruden, 1977), compromising cross-pollination between different individuals and favoring inbreeding depression (Morales & Galetto, 2003; Blambert et al., 2016). Our results corroborate the findings from other studies indicating detrimental effects of increasing CAD and aridity on pollen traits of other plant species (Quesada et al., 1995; Barnabás et al., 2008; Fang et al., 2010; Waser & Price, 2016; Descamps et al., 2018).

In contrast to our second prediction, we found that increasing CAD and aridity did not reduce the female reproductive success by open pollination and even had a positive effect. The seed-set in *T. palmadora* by open pollination increased when disturbance intensity increased. The results from the seed-set when pollinators are available may be due to the resilience of its most effective pollinators (Bustamante-Castillo et al., 2018). Some studies have demonstrated that hummingbirds can be highly resilient to different levels of disturbances due to their generalist behavior, as they might find alternative food resources regarding the intensity of the disturbance (Bustamante-Castillo et al., 2018). Ecosystems altered by human disturbances can be compensated with enhanced resource availability (Fontúrbel et al., 2017). Ecosystems with a more simplified structure usually display greater exposure to sunlight, which in turn favors the growth of generalist shade-intolerant plants that typically have large flower and fruit displays (Fontúrbel et al., 2017). Some plants, such as succulents, may produce more flowers in disturbed areas, as in some regions the vegetation is repeatedly cleared for the continuity of human activities, leaving the remaining vegetation exposed to higher solar radiation, and thus increase biomass production (Rodríguez-Oseguera et al., 2012). Hummingbirds are versatile in their foraging, having the ability to explore both specialized and non-specialized food resources (Machado, 2009). Specifically, *Chlorostilbon lucidus*, the main effective pollinator of *T. palmadora* (Locatelli & Machado, 1999), visits a high variety of floral types, with different colors and sizes (Machado, 2009), which could contribute to the maintenance of populations even when habitat structure is simplified by disturbance (Fontúrbel et al., 2017). Our results also corroborated other studies where pollination was generally more efficient in disturbed areas than in conserved ones (Rodríguez-Oseguera et al., 2012).

Meanwhile, increasing aridity positively affects the fruit-set by open pollination. This may be due to the increased availability of floral resources offered by *T. palmadora* in the driest areas of the park. Previous studies have shown that *T. palmadora* is more abundant in the driest areas of the semiarid region of Brazil (Ferreira et al., 2016). Greater plant abundance might imply a higher density of plants and thus more floral resources available, which increases its attractiveness and visitation of pollinators, thus favoring fruit formation (Dauber et al., 2010). In addition, it has been shown that despite some flower resources being reduced by aridity, such as nectar production, hummingbird visits could be high (Waser & Price, 2016).

Our study shows results that diverge with some studies and agree with others where the effect of disturbances and aridity has been evaluated for plant reproductive traits and success. For example, in the deciduous tree *Nothapodytes nimmoniana* (Icanaceae) in the Western Ghats, a mountain range in western India, disturbance reduced flower resources, which in turn caused changes in foraging patterns of the pollinators and thus, drastic reduction in reproductive success (Sharma et al., 2010). Otherwise, studies carried out with *Dactylhoriza hatagirea* (Orchidaceae) in the Himalayas, showed an inverse relationship between floral traits and reproductive success, since investing less in floral traits such as flower size can fool some pollinators, since it does not contain nectar and increased floral traits lead experienced pollinators to associate with a lack of nectar (Thakur et al., 2018). In the case of aridity, studies carried out with the common wildflower *Ipomopsis aggregata* (Polemoniaceae) in a Rocky Mountain meadow in the United States, showed that the production of pollen and nectar are reduced due to aridity and despite the fact that visits from pollinating hummingbirds stay high, less pollen is deposited and therefore the reproductive success is reduced (Waser & Price, 2016). Otherwise, each of the gradients affecting only one of the variables of reproductive success, that is, the CAD gradient affecting only seed-set and the aridity gradient affecting only fruit-set, may be due to the behavior of its pollinators and the plant water-use efficiency adaptations. Hummingbirds transport heterospecific pollen mixtures that have negative effects on the fitness of plants they visit (Fonseca et al., 2016). However, as few plants bloom during the dry season in the Caatinga dry forest (Locatelli & Machado, 1999; Lima et al., 2019), pollen transfer from *T. palmadora* might be highly efficient, especially in disturbed areas where the habitat structure is simplified (Fontúrbel et al., 2017), since their movements are influenced by nectar availability (Fonseca et al., 2015), and contribute to seed formation (Wang et al., 2017). Cactus have several adaptations that enable them to have good water-use efficiency (Snyman, 2013; Gargouri et al., 2021), and as *T. palmadora* dominates and proliferates in the driest areas (Ferreira et al., 2016), it could probably have adaptations that supply enough water for fruit formation.

Regarding our third prediction, we found no association between increasing CAD and aridity with female reproductive success when pollinators are not present, i.e. by spontaneous self-pollination. In contrast, other studies have shown that self-pollination success is higher in disturbed areas, as pollinators become scarce and thus outcrossing between different individuals is limited (Ortíz et al., 2010; Chen et al., 2016). In addition, self-pollination might also be favored with aridity, as some studies have shown that pollinator diversity and activity might decrease with increasing aridity, compromising natural pollinator services (e.g. Devoto et al., 2009; Maron et al., 2014; Gibson-Forty et al., 2020). Nevertheless, none of these situations account for pollination patterns of *T. palmadora* in our study area. This could be because the abundance and activity of the main pollinators of *T. palmadora* are not limiting in the driest areas of the park (see above), thus ensuring the reproduction of the species without the need to increase self-pollination (Sukumaran et al., 2020).

5. Conclusions

Shortly, we reported that fruit-set when pollinators are increased with increasing aridity, regardless the values of pollen traits decreased. Similarly, seed formation when pollinators are present increased with increasing CAD, regardless the values of pollen traits decreased. This means that even though pollen traits are reducing with higher CAD and aridity, pollination effectiveness of *T. palmadora* is maintained or even increased in the most arid and disturbed areas of the park. Thus, we show that in terms of pollination effectiveness, plant populations of *T. palmadora* might even be adapted to disturbance and aridity. Furthermore, since the impacts of CAD and climate change may differ between different groups of plants, future studies of the interaction effects between disturbance and climate change in plant-pollinator interactions should be conducted.

CRediT authorship contribution statement

Diego Centeno-Alvarado: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, review & editing. **Jéssica Luiza S. Silva:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing. **Oswaldo Cruz-Neto:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing. **Xavier Arnan:** Formal analysis, Investigation, Methodology, Writing – review & editing. **Ariadna Valentina Lopes:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing, Acquisition, Project administration, Supervision, Validation.

Declaration of Competing 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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Appendix A. Supplementary material

Supplementary data to this article was submitted with this manuscript.

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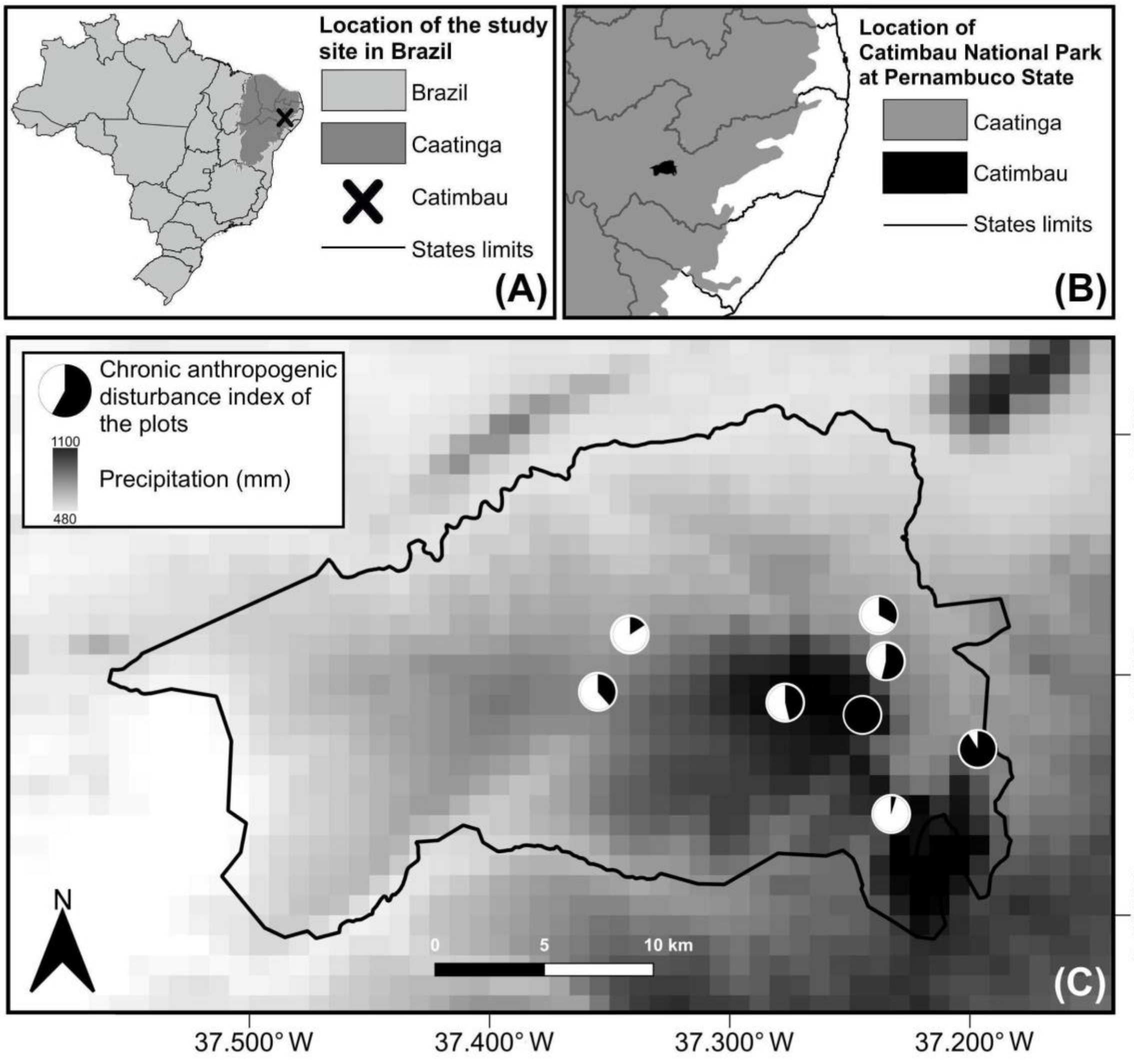

Fig. 2. Representation of the study site at different spatial scales: Brazil (A), Pernambuco state (B), and distribution of the eight plots surveyed in the Catimbau National Park (C). The circles indicate the disturbance intensity of the plots (range: 2.7 - 58.1), with the higher proportion of black indicating higher disturbance. The white to black background indicates the gradient of mean annual precipitation in the park (WorldClim version 2.1 climate data for 1970-2000 - Fick & Hijmans, 2017).

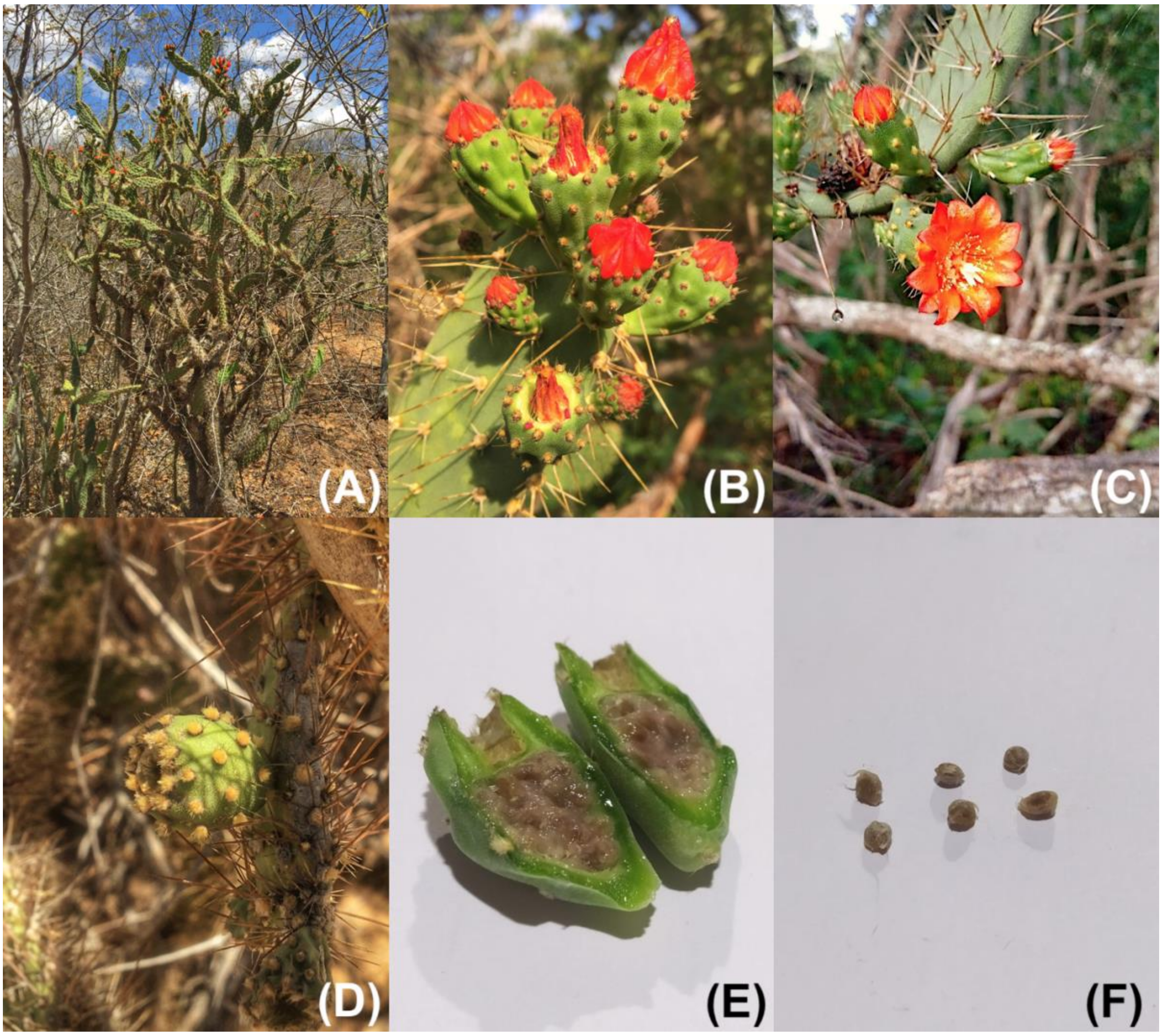

Fig. 3. *Tacinga palmadora*: Whole plant (A), flower buds (B), flowers and flower buds (C), fruit (D), open fruit (E), and seeds (F). (Credits for images: A, B, and D by Diego Centeno-Alvarado; C by Francisca Raimunda de Oliveira; E and F by Adrielle Leal).

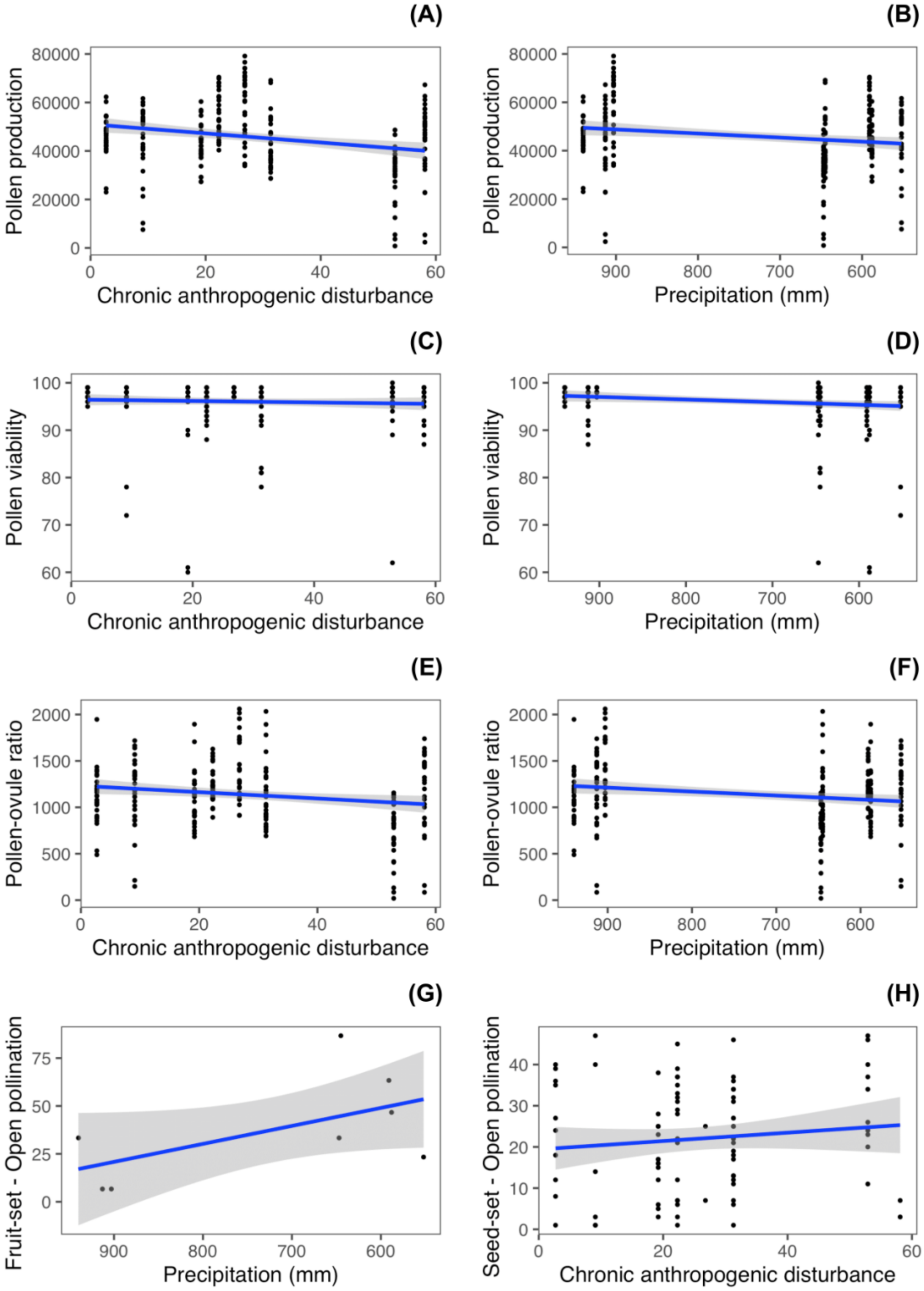

Fig. 4. Significant effects of chronic anthropogenic disturbance and precipitation on the floral traits and reproductive output of *Tacinga palmadora* in Catimbau NP, northeast Brazil, according to the model selection approach.

Table 1. Best-supported models (ΔAICc < 2) analyzing the effects of chronic anthropogenic disturbance (CAD) and precipitation (PRE) on the pollen traits and the reproductive success of *Tacinga palmadora* in Catimbau NP, northeast Brazil.

Response variable	Variables selected	df	AICc	ΔAICc	Weight	R^2
Floral traits						
Pollen production	PRE	5	5208.3	0.61	0.26	0.26
	CAD	5	5209.0	1.27	0.19	0.26
	CAD + PRE	6	5209.0	1.27	0.19	0.27
Pollen viability	PRE	4	1624.6	0.24	0.33	7.6×10^{-3}
	CAD	4	1626.3	1.87	0.15	8.3×10^{-4}
	CAD + PRE	5	1626.3	1.93	0.14	9.3×10^{-3}
Pollen-ovule ratio	PRE	5	3483.6	1.07	0.23	0.18
	CAD	5	3483.7	1.17	0.22	0.18
	CAD + PRE	6	3484.3	1.75	0.16	0.19
Reproductive success						
Fruit-set by open pollination	PRE	2	85.2	0.00	0.92	0.94
Seed-set by open pollination	CAD	5	729.3	1.27	0.26	0.01

Appendix A. Supplementary material

Table 2. Pollen traits measured for *Tacinga palmadora* (Cactaceae) in the surveyed plots at Catimbau National Park, Pernambuco, Brazil.

Plot	Chronic anthropogenic disturbance index	Precipitation	Individual	Flower	Pollen grains	Pollen-ovule ratio	Pollen viability (%)
P02	52.9	647	1	1	792	19.3	62.3
P02	52.9	647	1	2	38698.8	1105.7	98.2
P02	52.9	647	2	3	31624.4	608.2	98.5
P02	52.9	647	2	4	35603.1	936.9	95.4
P02	52.9	647	2	5	48647.4	1131.3	98.8
P02	52.9	647	3	6	34742.4	827.2	97.7
P02	52.9	647	3	7	38496	874.9	99.2
P02	52.9	647	4	8	30424.8	780.1	99.3
P02	52.9	647	4	9	30420.9	894.7	98.4
P02	52.9	647	4	10	37062.9	1029.5	99.5
P02	52.9	647	5	11	41256.6	877.8	96.8
P02	52.9	647	5	12	25110.4	660.8	98.0
P02	52.9	647	6	13	5454	133.0	92.3
P02	52.9	647	6	14	32751	536.9	95.0
P02	52.9	647	6	15	17538	407.9	97.3
P02	52.9	647	7	16	18720	416.0	97.7
P02	52.9	647	7	17	33647.9	820.7	96.0
P02	52.9	647	7	18	27382.8	652.0	98.3
P02	52.9	647	7	19	36260.4	614.6	95.2
P02	52.9	647	7	20	35262.2	860.1	98.2
P02	52.9	647	8	21	37002.4	1156.3	98.8
P02	52.9	647	8	22	3649	84.9	88.9
P02	52.9	647	9	23	40152.8	803.1	97.3
P02	52.9	647	9	24	41727	1069.9	97.5
P02	52.9	647	9	25	29886	597.7	98.5
P02	52.9	647	9	26	32216.4	826.1	96.3
P02	52.9	647	10	27	31467.8	828.1	99.1
P02	52.9	647	10	28	46699.2	1037.8	98.0

P02	52.9	647	10	29	29576.7	672.2	98.3
P02	52.9	647	10	30	12464.4	289.9	94.5
P04	22.3	591	1	1	68195.4	1136.6	96.8
P04	22.3	591	1	2	58915.2	1550.4	93.4
P04	22.3	591	1	3	62340	1387.3	88.2
P04	22.3	591	2	4	52841	1228.9	93.5
P04	22.3	591	2	5	43598.7	990.9	97.4
P04	22.3	591	2	6	52603.2	1119.2	93.3
P04	22.3	591	3	7	50138	983.1	96.0
P04	22.3	591	3	8	62535.6	1097.1	97.3
P04	22.3	591	3	9	66749.4	1628.0	96.6
P04	22.3	591	3	10	69894.4	1226.2	97.0
P04	22.3	591	3	11	44378.5	1167.9	98.1
P04	22.3	591	4	12	47219.2	1242.6	98.7
P04	22.3	591	4	13	55787.2	1267.9	98.9
P04	22.3	591	4	14	40342	1152.6	97.7
P04	22.3	591	4	15	42660	1185.0	97.9
P04	22.3	591	5	16	62163.9	1516.2	91.6
P04	22.3	591	5	17	45889.6	1092.6	97.9
P04	22.3	591	5	18	65197.8	1207.4	97.6
P04	22.3	591	5	19	53071.2	1153.7	95.0
P04	22.3	591	6	20	56955.6	1356.1	98.6
P04	22.3	591	6	21	48180	892.2	96.8
P04	22.3	591	6	22	70437	1280.7	96.2
P04	22.3	591	7	23	46941.5	1235.3	97.1
P04	22.3	591	7	24	60910.8	1107.5	97.6
P04	22.3	591	8	25	68026.6	1582.0	95.5
P04	22.3	591	8	26	52417	1497.6	94.7
P04	22.3	591	9	27	49539.6	1100.9	90.6
P04	22.3	591	9	28	45805.5	1090.6	97.4
P04	22.3	591	10	29	43476.4	1175.0	98.2
P04	22.3	591	10	30	49928.2	1085.4	94.8
P17	2.7	940	1	1	43318	1031.4	99.0
P17	2.7	940	1	2	24460.2	531.7	98.2

P17	2.7	940	1	3	54447.6	907.5	98.9
P17	2.7	940	2	4	44390	1387.2	98.0
P17	2.7	940	2	5	54289.5	1180.2	98.1
P17	2.7	940	2	6	49343	1049.9	97.0
P17	2.7	940	3	7	42593	1120.9	97.8
P17	2.7	940	3	8	49184.7	894.3	98.9
P17	2.7	940	3	9	45295.2	1053.4	96.9
P17	2.7	940	3	10	47011.7	1205.4	98.6
P17	2.7	940	4	11	41006	1079.1	96.1
P17	2.7	940	4	12	62311.8	1947.2	97.2
P17	2.7	940	5	13	48351	1343.1	97.6
P17	2.7	940	5	14	47328	1075.6	98.4
P17	2.7	940	5	15	40541.7	881.3	98.6
P17	2.7	940	6	16	42136.2	1027.7	95.9
P17	2.7	940	6	17	39818.1	1076.2	96.6
P17	2.7	940	6	18	60315.3	1402.7	97.1
P17	2.7	940	7	19	41935.8	1048.4	98.4
P17	2.7	940	7	20	54494.7	1434.1	97.4
P17	2.7	940	7	21	47959	1229.8	98.6
P17	2.7	940	8	22	48787.2	1161.6	98.7
P17	2.7	940	8	23	23002.2	489.4	95.1
P17	2.7	940	8	24	44200	1194.6	97.4
P17	2.7	940	9	25	43618.3	969.3	97.1
P17	2.7	940	9	26	48396	1273.6	98.3
P17	2.7	940	9	27	52095.8	854.0	98.9
P17	2.7	940	9	28	54213.3	1355.3	96.8
P17	2.7	940	10	29	46272.6	826.3	97.1
P17	2.7	940	10	30	51728	1124.5	96.8
P22	9.1	552	1	1	56498.4	1569.4	98.3
P22	9.1	552	1	2	61638.1	1503.4	97.9
P22	9.1	552	1	3	56572.8	1663.9	97.7
P22	9.1	552	2	4	55707.2	1466.0	98.4
P22	9.1	552	2	5	41769	1018.8	97.5
P22	9.1	552	2	6	51681.6	1148.5	97.8

P22	9.1	552	3	7	53265	1065.3	97.8
P22	9.1	552	3	8	24320.7	810.7	98.8
P22	9.1	552	4	9	7533.6	147.7	78.0
P22	9.1	552	4	10	50995.8	1342.0	98.2
P22	9.1	552	5	11	53426.7	1335.7	98.5
P22	9.1	552	5	12	40572.8	863.6	96.7
P22	9.1	552	5	13	42824.8	1189.6	98.3
P22	9.1	552	5	14	31651.8	904.3	98.8
P22	9.1	552	6	15	53987.4	1384.3	97.8
P22	9.1	552	6	16	38607.8	858.0	95.4
P22	9.1	552	6	17	56151.2	1369.5	97.4
P22	9.1	552	6	18	21283.1	591.2	97.5
P22	9.1	552	7	19	55515.6	1354.0	97.0
P22	9.1	552	7	20	10231.2	213.2	72.1
P22	9.1	552	8	21	47040	904.6	98.2
P22	9.1	552	8	22	41183.1	1113.1	97.4
P22	9.1	552	8	23	45512.6	1197.7	96.4
P22	9.1	552	9	24	59018.4	1639.4	97.4
P22	9.1	552	9	25	52258	1306.5	99.2
P22	9.1	552	9	26	56362.7	1342.0	98.5
P22	9.1	552	10	27	55372.4	1178.1	96.3
P22	9.1	552	10	28	60118.2	1717.7	97.1
P22	9.1	552	10	29	37100	976.3	95.4
P22	9.1	552	10	30	52785.9	1256.8	97.9
P25	19.2	588	1	1	45402	825.5	98.6
P25	19.2	588	1	2	60375	1284.6	98.7
P25	19.2	588	2	3	39020.3	1258.7	97.6
P25	19.2	588	2	4	56842.5	1894.8	61.1
P25	19.2	588	3	5	42142.8	936.5	99.0
P25	19.2	588	3	6	50176	1393.8	98.0
P25	19.2	588	3	7	29233.6	790.1	89.3
P25	19.2	588	3	8	37382.8	1168.2	98.8
P25	19.2	588	4	9	27265.8	717.5	97.9
P25	19.2	588	4	10	33716.1	963.3	98.1

P25	19.2	588	4	11	38841.6	903.3	98.0
P25	19.2	588	5	12	44528.4	1113.2	98.1
P25	19.2	588	5	13	42064.8	914.5	98.6
P25	19.2	588	5	14	40664.4	1196.0	98.6
P25	19.2	588	6	15	50783.2	1372.5	98.0
P25	19.2	588	6	16	39978.8	951.9	98.8
P25	19.2	588	6	17	48031.2	1372.3	97.5
P25	19.2	588	6	18	44646	1144.8	97.7
P25	19.2	588	7	19	54606.5	1706.5	59.8
P25	19.2	588	7	20	37220.4	907.8	98.7
P25	19.2	588	7	21	45084.3	1252.3	98.2
P25	19.2	588	7	22	56273.5	1250.5	99.2
P25	19.2	588	7	23	45404.8	1375.9	96.1
P25	19.2	588	8	24	39248.6	1060.8	97.1
P25	19.2	588	8	25	44833	845.9	96.5
P25	19.2	588	8	26	27337.9	683.5	97.3
P25	19.2	588	9	27	43663.4	1149.0	98.6
P25	19.2	588	9	28	38377.6	1128.8	96.9
P25	19.2	588	10	29	29159.1	747.7	90.4
P25	19.2	588	10	30	39942	951	98.0
P26	31.3	645	1	1	68138.4	1892.7	97.6
P26	31.3	645	1	2	33272.2	739.4	80.9
P26	31.3	645	2	3	39223.6	1032.2	98.8
P26	31.3	645	2	4	31140	915.9	78.0
P26	31.3	645	2	5	33154	896.1	98.6
P26	31.3	645	2	6	57449.7	1336.0	96.2
P26	31.3	645	3	7	47684.7	1222.7	91.3
P26	31.3	645	3	8	39192	870.9	97.1
P26	31.3	645	3	9	35923.3	764.3	91.8
P26	31.3	645	4	10	28724	897.6	97.2
P26	31.3	645	4	11	36385.9	1010.7	95.9
P26	31.3	645	5	12	52759.2	1598.8	98.1
P26	31.3	645	5	13	47028.8	1383.2	98.1
P26	31.3	645	5	14	47197.8	1388.2	97.9

P26	31.3	645	5	15	39709.8	968.5	93.4
P26	31.3	645	5	16	43423.8	1315.9	98.4
P26	31.3	645	6	17	42934.1	1129.8	92.4
P26	31.3	645	6	18	53405.6	1780.2	97.0
P26	31.3	645	6	19	51120.9	1420.0	97.1
P26	31.3	645	6	20	28641.6	795.6	81.2
P26	31.3	645	7	21	37029.3	925.7	92.8
P26	31.3	645	7	22	36428.7	934.1	96.6
P26	31.3	645	7	23	40104.2	1114.0	97.5
P26	31.3	645	8	24	54101.4	1319.6	96.9
P26	31.3	645	8	25	39498.2	1161.7	97.7
P26	31.3	645	9	26	37932.3	1185.4	95.0
P26	31.3	645	9	27	69130.5	2033.3	96.4
P26	31.3	645	10	28	32520.6	691.9	80.9
P26	31.3	645	10	29	33868.8	787.7	82.0
P26	31.3	645	10	30	35227.4	819.2	97.4
P27	26.8	903	1	1	67758.8	1411.6	97.8
P27	26.8	903	1	2	76608	2016.0	99.1
P27	26.8	903	1	3	72345.3	1955.3	98.1
P27	26.8	903	1	4	69226.5	1412.8	97.1
P27	26.8	903	1	5	79154.9	1759.0	97.9
P27	26.8	903	2	6	60745.2	1412.7	98.3
P27	26.8	903	2	7	70968.6	1730.9	98.7
P27	26.8	903	3	8	67408.2	1728.4	97.9
P27	26.8	903	3	9	66840.1	1261.1	97.2
P27	26.8	903	3	10	70858.5	1728.3	97.4
P27	26.8	903	3	11	54881.5	1276.3	98.4
P27	26.8	903	4	12	43337	1083.4	98.5
P27	26.8	903	4	13	38009.1	1027.3	98.3
P27	26.8	903	5	14	34647.2	911.8	98.2
P27	26.8	903	5	15	47397	1102.3	97.7
P27	26.8	903	5	16	70397.1	1955.5	98.4
P27	26.8	903	6	17	47334	1154.5	97.7
P27	26.8	903	6	18	66990.3	1288.3	98.0

P27	26.8	903	6	19	62875.8	1462.2	98.1
P27	26.8	903	7	20	60380.4	1207.6	97.5
P27	26.8	903	7	21	50641.5	1150.9	98.4
P27	26.8	903	8	22	67885.5	1697.1	97.1
P27	26.8	903	8	23	64147.6	1733.7	98.3
P27	26.8	903	9	24	74117.7	1723.7	96.7
P27	26.8	903	9	25	48755	1218.9	97.2
P27	26.8	903	9	26	41430.5	1150.9	97.1
P27	26.8	903	10	27	33864.3	915.3	98.3
P27	26.8	903	10	28	70652.4	1859.3	99.2
P27	26.8	903	10	29	55895.2	1397.4	99.1
P27	26.8	903	10	30	74146.8	2059.6	98.3
P30	58.1	913	1	1	51034.2	1000.7	97.9
P30	58.1	913	1	2	2354.7	84.1	86.7
P30	58.1	913	2	3	59297.7	1602.6	97.5
P30	58.1	913	2	4	40853.2	833.7	94.9
P30	58.1	913	2	5	51497.6	1197.6	96.1
P30	58.1	913	2	6	50013.7	1562.9	99.0
P30	58.1	913	3	7	36828	1116.0	90.9
P30	58.1	913	3	8	22897.6	693.9	94.8
P30	58.1	913	3	9	57385.5	1739.0	98.4
P30	58.1	913	4	10	67284.3	1431.6	98.5
P30	58.1	913	4	11	55611.6	1588.9	98.1
P30	58.1	913	4	12	46654.8	1458.0	96.7
P30	58.1	913	4	13	32334	829.1	98.0
P30	58.1	913	5	14	45150.3	1290.0	98.9
P30	58.1	913	5	15	48686.4	1475.4	98.6
P30	58.1	913	6	16	53472	1445.2	97.0
P30	58.1	913	6	17	44434.2	1481.1	94.9
P30	58.1	913	6	18	52139.4	1086.2	98.6
P30	58.1	913	7	19	62616.8	1456.2	98.9
P30	58.1	913	7	20	22748.1	669.1	89.0
P30	58.1	913	7	21	54145.8	1320.6	95.6
P30	58.1	913	7	22	34794.2	809.2	95.7

P30	58.1	913	8	23	36154.4	1033.0	88.8
P30	58.1	913	8	24	45503.9	1264.0	97.4
P30	58.1	913	9	25	5357.8	157.6	91.8
P30	58.1	913	9	26	57222	1634.9	98.1
P30	58.1	913	10	27	61124.1	1567.3	97.9
P30	58.1	913	10	28	47516.4	1319.9	98.1
P30	58.1	913	10	29	33635	885.1	98.2
P30	58.1	913	10	30	50568.2	1487.3	98.9

Table 3. Female reproductive success: Fruit-set in *Tacinga palmadora* (Cactaceae) plants in the surveyed plots at Catimbau National Park, Pernambuco, Brazil.

Plot	**Chronic anthropogenic disturbance index**	**Precipitation (mm)**	**Open pollination**		**Spontaneous self-pollination**	
			Fruit formed / Pre-anthesis flower buds marked	**Fruit-set (%)**	**Fruit formed / Pre-anthesis flower buds marked and bagged**	**Fruit-set (%)**
P02	52.9	647	10/30	33.3	2/30	6.7
P04	22.3	591	19/30	63.3	1/30	3.33
P17	2.7	940	10/30	33.3	1/30	3.33
P22	9.1	552	7/30	23.3	3/30	10.0
P25	19.2	588	14/30	46.7	1/30	3.33
P26	31.3	645	26/30	86.7	1/30	3.33
P27	26.8	903	2/30	6.7	3/30	10.0
P30	58.1	913	2/30	6.7	4/30	13.3

Table 4. Female reproductive success: Seed-set in *Tacinga palmadora* (Cactaceae) in the surveyed plots at Catimbau National Park, Pernambuco, Brazil.

Plot	**Chronic anthropogenic disturbance index**	**Precipitation (mm)**	**Experiment (Openl pollination: O; Spontaneous self-pollination: S)**	**Sampled individual**	**Number of fruits**	**Number of seeds**
P02	52.9	647	O	1	6	47
P02	52.9	647	O	3	15	37

P02	52.9	647	O	3	16	46
P02	52.9	647	O	5	22	20
P02	52.9	647	O	5	23	26
P02	52.9	647	O	5	24	11
P02	52.9	647	O	5	25	23
P02	52.9	647	O	5	26	34
P02	52.9	647	O	5	27	40
P02	52.9	647	O	5	28	24
P04	22.3	591	O	2	7	37
P04	22.3	591	O	2	8	32
P04	22.3	591	O	2	10	7
P04	22.3	591	O	2	11	7
P04	22.3	591	O	2	12	22
P04	22.3	591	O	2	13	31
P04	22.3	591	O	2	14	6
P04	22.3	591	O	2	15	39
P04	22.3	591	O	2	16	37
P04	22.3	591	O	2	17	29
P04	22.3	591	O	4	19	1
P04	22.3	591	O	4	20	3
P04	22.3	591	O	4	21	35
P04	22.3	591	O	5	22	21
P04	22.3	591	O	5	23	12
P04	22.3	591	O	5	26	33
P04	22.3	591	O	5	28	45
P04	22.3	591	O	10	29	28
P04	22.3	591	O	10	30	37
P17	2.7	940	O	1	1	8
P17	2.7	940	O	2	3	36
P17	2.7	940	O	2	4	27
P17	2.7	940	O	2	5	24
P17	2.7	940	O	2	6	35
P17	2.7	940	O	2	7	39
P17	2.7	940	O	2	8	18

P17	2.7	940	O	2	9	1
P17	2.7	940	O	3	12	12
P17	2.7	940	O	3	14	40
P22	9.1	552	O	1	1	40
P22	9.1	552	O	1	2	1
P22	9.1	552	O	2	11	1
P22	9.1	552	O	2	13	3
P22	9.1	552	O	2	14	1
P22	9.1	552	O	3	17	14
P22	9.1	552	O	3	18	47
P25	19.2	588	O	2	4	25
P25	19.2	588	O	2	5	16
P25	19.2	588	O	2	6	25
P25	19.2	588	O	3	7	17
P25	19.2	588	O	3	8	23
P25	19.2	588	O	3	9	6
P25	19.2	588	O	3	10	5
P25	19.2	588	O	3	11	15
P25	19.2	588	O	3	12	28
P25	19.2	588	O	3	13	3
P25	19.2	588	O	3	15	38
P25	19.2	588	O	4	18	16
P25	19.2	588	O	4	19	12
P25	19.2	588	O	4	20	17
P26	31.3	645	O	1	1	7
P26	31.3	645	O	1	2	13
P26	31.3	645	O	1	3	25
P26	31.3	645	O	1	4	22
P26	31.3	645	O	1	5	13
P26	31.3	645	O	1	6	13
P26	31.3	645	O	1	7	19
P26	31.3	645	O	1	8	46
P26	31.3	645	O	1	9	12
P26	31.3	645	O	1	10	18

P26	31.3	645	O	1	11	17
P26	31.3	645	O	1	12	34
P26	31.3	645	O	1	13	25
P26	31.3	645	O	1	14	13
P26	31.3	645	O	1	15	6
P26	31.3	645	O	1	16	31
P26	31.3	645	O	1	17	37
P26	31.3	645	O	2	18	27
P26	31.3	645	O	2	19	27
P26	31.3	645	O	2	20	32
P26	31.3	645	O	2	21	1
P26	31.3	645	O	2	22	34
P26	31.3	645	O	2	23	34
P26	31.3	645	O	2	24	11
P26	31.3	645	O	4	28	21
P26	31.3	645	O	4	29	36
P27	26.8	903	O	1	2	7
P27	26.8	903	O	1	7	25
P30	58.1	913	O	1	1	7
P30	58.1	913	O	4	18	3
P02	52.9	647	S	5	24	14
P02	52.9	647	S	5	27	32
P04	22.3	591	S	5	25	36
P17	2.7	940	S	1	2	27
P22	9.1	552	S	2	4	3
P22	9.1	552	S	2	5	1
P22	9.1	552	S	2	9	1
P25	19.2	588	S	2	8	5
P26	31.3	645	S	2	8	28
P27	26.8	903	S	2	13	4
P27	26.8	903	S	2	17	2
P27	26.8	903	S	2	19	1
P30	58.1	913	S	1	7	2
P30	58.1	913	S	3	13	1

P30	58.1	913	S	3	15	2
P30	58.1	913	S	3	16	2

5 CHAPTER 2 – MANUSCRIPT TO BE SUBMITTED TO THE JOURNAL BIOLOGICAL CONSERVATION

Climate change will reduce suitable habitat for dry forest endemic species: A species distribution modeling approach using plant-pollinator interactions

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Abstract

Climate change modifies geographic ranges, seasonal activities, and biological interactions - key components of species ecological niche. Alterations in distribution ranges could decrease the size of the populations and thus threaten the persistence of the species. Here, we seek to understand the effects of climate change on the suitable areas for *T. palmadora* (Cactaceae), an endemic species of the Caatinga dry forest, including plant-pollinator interactions in the models. We first modeled the current and future distribution of both *T. palmadora* and its main effective pollinator, the hummingbird *Chlorostilbon lucidus*, separately using only climatic variables. Then we modeled *T. palmadora* current and future distribution using *C. lucidus* distribution as an input layer alongside the climatic variables. We used optimistic (RCP4.5) and pessimistic (RCP8.5) climate change scenarios. In general, models that include plant-pollinator interactions performed greater, demonstrating that suitable areas of *T. palmadora* will be reduced in the near future. Models using only climatic variables resulted in significant increases in the suitable areas for *T. palmadora* (12.66% - RCP4.5; 16.82% - RCP8.5) and *C. lucidus* (14.98% - RCP4.5; 1.94% - RCP8.5). On the other hand, models that include plant-pollinator interaction resulted in significant decreases in suitable areas for *T. palmadora* (32.51% - RCP4.5; 8.31% - RCP8.5). Our study highlights the importance of considering biotic interactions on species distribution models and shows that *T. palmadora* may lose a part of its climatic envelope, already restricted by its endemism, generating negative cascade effects on the region.

Keywords: Biotic interactions, ecological niche modeling, geographic distributions, global change, tropical dry forest

Introduction

Current anthropogenic greenhouse gases emissions (hereafter referred to as GHG) are the highest in history (IPCC, 2014). The high concentration of GHG, such as carbon dioxide, methane and nitrous oxide, is causing an unequivocal warming of the climate system, which is also evidenced in the increasing temperature of the oceans and the atmosphere (IPCC, 2014). As a consequence, several organisms may exhibit shifts in their geographic ranges, seasonal activities, migration patterns, abundance and interactions (Warren et al., 2011; IPCC, 2014 Gómez-Ruiz & Lacher Jr., 2019). Climate change can exacerbate the effect of other pressures, such as degradation and fragmentation (Scheffers et al., 2016; Malhi et al., 2020).

The reduction and fragmentation of the distribution ranges could decrease the size of the populations and thus threaten the persistence of the species (Velásquez-Tibatá et al., 2011; IPCC, 2014). Reductions in the size of the distribution ranges are particularly harmful for endemic species, which already have small ranges (Velásquez-Tibatá et al., 2011). On the other hand, each species may respond differently to changes, causing the disruption of some interactions between key species (Erauskin-Extramiana et al., 2019). Furthermore, the redistribution of species is likely to accelerate in the near future and it is possible that the new regions to which the species move provide less suitable habitats than those in their current distribution (Velásquez-Tibatá et al., 2011; Jarvie and Svenning, 2018).

Species distribution models (SDM) are used to understand the distribution of species in terms of space and time, addressing issues such as impacts of global climate change on species distribution and quantification of environmental niches, which are important for conservation planning (Palacio & Girini, 2018). SDMs determine species habitat suitability based on the relationships of species occurrences with environmental variables (Palacio & Girini, 2018). SDMs usually do not consider biotic interactions (Palacio & Girini, 2018), however, geographical distribution of species is influenced by biotic interactions within their habitats, as biotic factors are important niche requirements (De Araujo et al., 2014; Silva et al., 2014). In fact, several studies have demonstrated that including biotic interactions in SDMs improve predictions of the species distributions, as biotic interactions are relevant for SDMs at large scales and SDMs performed only with abiotic variables generate only a partial representation of the species distribution (Araujo & Luoto, 2007; Heikkinen et al., 2007; Bateman et al., 2012; Hof et al., 2012; Giannini et al., 2013; Araujo et al., 2014; Araujo & Rozenfeld, 2014; Duffy & Johnson, 2017; Atauchi et al., 2018; Palacio & Girini, 2018). Biotic interactions can be included in SDMs in different ways, for example as co-occurrences (Meier et al., 2010), frequency of occurrence of the interacting species (Heikkinen et al., 2007) or with the current and future projected distribution of the interacting species (Araújo & Luoto, 2007; Bateman et al., 2012; Hof et al., 2012; Giannini et al., 2013; De Araújo et al., 2014; Duffy & Johnson, 2017; Atauchi et al. , 2018; Palacio & Girini, 2018). Studies commonly use the potential distribution of the interacting species, since the distribution has been shown to be highly correlated with the abundance of the species (VanDerWal et al., 2009; Kulhanek et al., 2011; Oliver et al., 2012) and it may be more useful when the distribution of any of the interacting species is not completely known (Giannini et al., 2013). In some studies, using the distribution of the interacting species as a predictor variable for some species may result in better performance of SDMs (e.g. Giannini et al., 2013).

Pollination is an important biotic interaction to evaluate in SDMs since pollinators are considered components of the ecological niche of some plants due to fruit and seed production (e.g. Giannini et al., 2013; Duffy & Jonhson, 2017; Tsiftsis &

Djordjević, 2020). Considering that more than 80% of angiosperms depend on pollinators (Ollerton et al., 2011) and the effects that this may have on modulating plant populations, the geographic distributions of these plants may be shaped not only by abiotic factors, but also by the distributions of those mutualists (Duffy & Johnson, 2017; Dormann et al., 2018).

In the Caatinga dry forest, one of the largest and most continuous seasonally dry tropical forest (SDTF) in America, located in northeastern Brazil (Aguiar et al., 2002; Silva et al., 2017), pollination systems are highly diversified (Silva et al., 2020). However, as other tropical dry forests, it is highly vulnerable to climate change, as they host high population densities and most of the forest area is converted for agriculture and livestock grazing (Silva et al., 2017; Stan & Sanchez-Azofeifa, 2019). A recent study (Silva et al., 2019) has shown that endemic plant species in the Caatinga will most likely lose suitable habitats due to climatic change, even in conservative future scenarios. These reductions will probably be even higher for endemic plant species with specialized reproductive traits (Silva et al., 2019). Reductions of areas with suitable climatic conditions might have consequences in the biological dynamics of the Caatinga dry forest, disrupting key ecological interactions (e.g. pollination) and compromising the maintenance and stability of plant and animal communities in the region (Silva et al., 2019).

Considering the importance of including biotic interactions in SDMs to enhance ecological knowledge of species niche, we seek to understand the effects of climate change, under both optimistic and pessimistic scenarios, on the range and distribution of suitable habitat for *Tacinga palmadora,* an endemic cactus and an important animal food resource, especially during dry season, in the Caatinga dry forest. For this, we aimed to compare the performances and suitable areas of species distribution models using only climatic variables and models using climatic variables and pollinator interactions. We also aimed to identify important variables explaining T. palmadora distribution.

Methods

Studied species and its distribution data

Tacinga palmadora (subfamily Opuntioideae) is a shrubby cactus endemic to the Caatinga dry forest with wide occurrence in the region, and is of great importance due to its use as a food resource for nectar-feeding animals and for livestock, especially in periods of droughts (Locatelli & Machado, 1999; Lima et al., 2019; Georgin et al., 2019). In contrast to the majority of the Caatinga flowering species, it flowers during dry season, from June to November (Locatelli & Machado, 1999). The species is self-compatible and self-spontaneous (Machado et al., 2006), however, we have seen that the reproductive success is greater with the contribution of pollinators (DCA personal observations). *Tacinga palmadora* is an ornithophilous species, presenting contrasting petal coloration and high concentrations of sugar, and is pollinated mainly by the hummingbird *Chlorostilbon lucidus* (Shaw, 1812) (Trochilidae), its most frequent and effective pollinator (Locatelli & Machado, 1999). The species *C. lucidus* is resident and remains throughout the year, due to the supply of compatible food resources during the year (Machado, 2009).

We gathered georeferenced data of *Tacinga palmadora* within the phytogeographic domain of the Caatinga from the Global Biodiversity Information Facility (GBIF - http://www.gbif.org). We filtered the data to include only records where the species occur and exclude repeated data. Using these filters, we obtained a total of 133 occurrence records for the species (Fig. 5). We also gathered georeferenced data from *T. palmadora* most frequent and main effective pollinator, the hummingbird *Chlorostilbon lucidus* (Locatelli & Machado, 1999), using the same filters and database, obtaining a total of 546 occurrence records for the species (Fig. 5). The complete information of the georeferenced data for these species can be found in the Supplementary Material (Appendix A supplementary information, Tables 8-9).

Climatic variables

We initially used the 19 bioclimatic variables with a 30 arc-sec spatial resolution (ca. 1 km^2), from the WorldClim 2.0 dataset (www.worldclim.org) (Giannini et al. 2013; Silva et al., 2014; Qin et al. 2017; Silva et al., 2019). Current climate data (Hijmans et al., 2005) are based on climatic information from the period 1970-2000, and climate projections for the future (Watanabe et al., 2010; Gent et al., 2011), for the period between 2070 and 2100, are based on the IPCC5 database, calibrated according to current climate information (Silva et al., 2019).

The current climate data are constructed with the monthly precipitation and mean, minimum, and maximum temperature (Hijmans et al., 2005). Future climate data are based on global models of oceanic circulation and atmospheric, terrestrial and marine biogeochemistry: CCSM4, which includes simulations for El Niño Southern Oscillation (ENSO) events (Gent et al., 2011), and MIROC-ESM, which includes simulations of terrestrial carbon cycling and vegetation dynamics (Watanabe et al., 2010). The two Representative Concentration Pathways (RCPs) future scenarios (4.5 and 8.5) are based on GHG emissions (related to data of atmospheric, oceanic and terrestrial biogeochemistry, solar radiation, etc.) (IPCC, 2014). The first one (RCP4.5) represents an optimistic scenario, where GHG emissions cause milder changes in the temperature, while the second one (RCP8.5) represents the most pessimistic scenario, where GHG emissions and changes in the temperature are the highest (IPCC, 2014).

We performed correlation tests with the 19 bioclimatic variables, with current and future (within or between CCSM4 and MIROC-ESM) scenarios, to exclude highly correlated variables (r > 0.9 Pearson correlation coefficient) (Qin et al., 2016; Silva et al., 2019). In total, a set of nine bioclimatic variables were retained: (1) annual mean temperature (BIO1), (2) isothermality (BIO3), (3) temperature seasonality (BIO4), (4) temperature annual range (BIO7), (5) annual precipitation (BIO12), (6) precipitation seasonality (BIO15), (7) precipitation of driest quarter (BIO17), (8) precipitation of warmest quarter (BIO18) and (9) precipitation of coldest quarter (BIO19).

Modeling potential species distribution including plant-pollinator interactions

We used the maximum entropy (MaxEnt) method to predict the most suitable areas of *T. palmadora* in the Caatinga dry forest using the MaxEnt v. 3.4.1 software (Phillips et al., 2020). The MaxEnt method uses presence-only data to estimate a species probability distribution by searching the probability distribution of maximum entropy (Phillips et al., 2006). We run each model for current and future (RCP4.5 and RCP8.5) scenarios 30 times, using the features in standard configuration and regularization multiplier (rm) = 1. First, we ran the models for the present and future potential distribution of *T. palmadora* and *C. lucidus*, separately, with the climatic variables only. Afterwards, the results of the potential distribution of *C. lucidus* were used as an input layer, together with the climatic variables within the models, to project the effects of climate change on the potential distribution of *T. palmadora* considering biotic interactions, since the potential distribution of the interacting species has been used as a proxy of biological interaction in several studies (Araújo & Luoto, 2007; Bateman et al., 2012; Hof et al., 2012; Giannini et al., 2013; De Araújo et al., 2014; Duffy & Johnson, 2017; Atauchi et al., 2018; Palacio & Girini, 2018). Even though some studies (Blanchet et al., 2020) claimed that spatial association is poor proxy for ecological interactions, we suppose that interaction occurs between them due to their phenological matches and because it has been shown that *C. lucidus* is a highly efficient species in the pollination of *T. palmadora* (Locatelli & Machado, 1999). The models for the current period and two future scenarios generated percent contribution of the variables to distribution of the species. Furthemore, with the generated models, we measured areas of occurrences and constructed maps with the probabilities of occurrence using the software QGIS 3.10 “A Coruña” (QGIS Development Team, 2019). Suitable habitat areas were defined as the ones with higher probability of occurrence (>80%) (Silva et al., 2019).

Statistical analyses

To assess the performances of all the models we calculated the mean area under the receiving operator curve (AUC), True Skill Statistics (TSS) and gain values. We used AUC to determine the best adjusted models, with values ranging from 0 to 1, and the latter representing perfect discrimination of suitable versus unsuitable areas for the species (Phillips et al., 2006; Qin et al., 2016; Silva et al., 2019). We used TSS values of each model to evaluate the performance of the models, as it is more realistic to AUC (e.g. Silva et al., 2019). Values of AUC and TSS higher than 0.7 represent an optimal performance (Silva et al., 2014). Therefore, between the models using only climatic variables and the models using climatic variables and pollinator interactions, we defined the best-supported models as those that resulted in higher values of AUC and TSS. Furthermore, we used gain values to determine the proximity between the models and the sampled data, with higher values indicating more proximity (Phillips et al., 2006).

To assess whether suitable habitat areas for *T. palmadora* and *C. lucidus* will be modified or not by climate change, we compared the suitable areas determined for the present with the areas from the two future climate change scenarios, using Kruskall-Wallis and Dunn tests in R (R Development Core Team, 2019), as the distribution of the data was non-parametric.

Results

Our results showed that isothermality, followed by annual precipitation, highly determined the current (49.1% and 21.7%, respectively) and future (RCP4.5 = 45.2% and 21.5%, respectively; RCP8.5 = 45.0% and 18.2, respectively) distribution range of *Tacinga palmadora*, using climatic variables only (Table 5). For the pollinator, the models showed that isothermality, annual precipitation and temperature seasonality, highly determined the current (50.0%, 12.8% and 24.3%, respectively) and future (RCP4.5 = ; 48.3%, 19.7% and 16.1%, respectively; RCP8.5 = 54.2%, 12.0% and 10.4%, respectively) distribution range of *C. lucidus*. Otherwise, the models using climatic and biotic variables showed that the interaction with the pollinator highly determines the current (87.0%) and future (RCP4.5 = 85.1%; RCP8.5 = 89.7%) distribution range of *T. palmadora* (Table 5).

In all of our models, AUC and TSS values showed high values (Table 6), representing an optimal performance. SDMs using pollinator interactions as an input layer showed better predictive performance in all scenarios, obtaining the highest TSS values (Table 6), representing better performance of SDMs with the inclusion of biotic interactions. Furthermore, gain values showed high proximity between the models and the sampled data (Table 6). As modeling experiments showed better performance including pollinator interactions (Table 6), we considered SDMs with biotic interactions more accurate and realistic. Comparing the two climate change future scenarios separately, with the inclusion of pollinator interactions, suitable habitats for *T. palmadora* will be most reduced under the optimistic climate change scenario (Table 7; Fig 6).

The models using only climatic variables resulted in significant increases of suitable areas for *T. palmadora* and *C. lucidus* under both optimistic (12.66% and 14.98%, respectively) and pessimistic (16.82% and 1.94%, respectively) climate change scenarios (Table 6; Figs. 6A-C and G-I). Pairwise comparisons using Dunn's test from the models using only climatic variables indicated that the projected future distribution areas of *T. palmadora* and *C. lucidus* are significantly larger from the current distribution in both optimistic (both p=<0.01) and pessimistic (both p=<0.01) climate change scenarios. The models including the pollinator interaction showed contrasting results with the models using only climatic variables, with suitable areas of *T. palmadora* reducing significantly in the future under both optimistic (32.51%) and pessimistic (8.31%) climate change scenarios (Table 6; Figs. 6D-F). Pairwise comparisons using Dunn's test indicated that the current distribution area of *T. palmadora*, from the models using climatic and biotic variables, is significantly larger from the projected future distribution in both optimistic (p=<0.01) and pessimistic (p=<0.01) climate change scenarios.

Discussion

Overall, our results highlight the importance of including biotic interactions while predicting species distributions. Our results showed that models including interaction with pollinators performed greater and that models using only climatic variables may lead to less realistic projections. Those best-supported models showed that the areas of suitable habitat for *T. palmadora* in the Caatinga dry forest will be reduced significantly in both scenarios of climate projections.

Based on the results from the best-supported models, our study showed that pollinator interactions mostly determined the distributions of the species. This could due to the fact that biotic interactions are an important niche requirement (De Araujo et al., 2014; Silva et al., 2014). Specifically, pollinators are considered key niche components for angiosperms due to their contribution to fruit and seed production (Duffy & Jonhson, 2017).

Models using only climatic variables predicted a significant increase in areas of suitable habitat for *T. palmadora*, while the inclusion of the interaction with pollinators in the models showed a significant reduction in areas of probable occurrence for the species. These results coincide with the results from other studies, where the inclusion of biotic factors generated divergent predictions from models run with only climatic variables (Araujo & Luoto, 2007; Bateman et al., 2012). Nevertheless, our results supported the idea that including biotic interactions in SDMs improve predictions of the species distributions (Araujo & Luoto, 2007; Heikkinen et al., 2007; Bateman et al., 2012; Hof et al., 2012; Giannini et al., 2013; Araujo et al., 2014; Araujo & Rozenfeld, 2014; Duffy & Johnson, 2017; Atauchi et al., 2018; Palacio & Girini, 2018). This can also be evidenced in the limitation of the species distribution range due to the loss of key mutualistic interactions (Duffy & Johnson, 2017).

Our best-supported models showed that suitable habitats for *T. palmadora* will be reduced in climate change projection, supporting the idea that global climate change causes a shift in the distribution of species (Williams et al., 2008). Even though the pollinator distribution range will increase, the maps showed that the pollinator distribution might diverge to the plant distribution, as it might be shifting to the north and northwest, while the plant distribution might be shifting to the southeast, to the coast region, as this area is most likely to be the least arid (Silva et al., 2019). This probably means the break of mutualism between the plant and its pollinator, since the areas of occurrence of both species tend to diverge. Furthermore, as shown by Silva et al. (2019), where plants endemic to the Caatinga dry forest are highly reproductively vulnerable even in more optimistic climate change projections and could lose their climatic envelope, the same occurred with *T. palmadora*. Our results corroborate the findings of other study in Mexico indicating reduction of areas of suitable habitat for other cacti species, an endangered and geographically rare globose cactus (*Coryphantha werdermannii*) (Martorell et al., 2014). The Caatinga dry forest is not only suffering high pressure from climate change and human disturbances, but it has also lost more than 50% of its original coverage due to the intensification and expansion of anthropogenic activities and currently less than 2% of the area is under protection (Silva et al., 2017; Fonseca et al., 2017). Populations of *T. palmadora* will most likely be reduced and several dynamics and ecosystem functioning will be altered. This will most likely have consequently have negative cascade effects on the region, as the species represents an important food source for nectar-feeding animals, especially during the dry season when food resources are scarce (Locatelli & Machado, 1999; Lima et al., 2019).

In conclusion, biotic interactions are a key component in species distribution models and when not considered, potential suitable areas could be overestimated. Furthemore, *T. palmadora* is vulnerable to future climate change and may lose a part of its climatic envelope. Since the effects of climate change may differ between different groups of plants and biological interactions, future studies on the effects of climate change on species distribution, considering biotic interactions, should be conducted. Landscape strategies, such as the creation and implementation of protected areas, could diminish the impacts of climate change on the species distribution ranges, as areas of suitable habitat could be maintained or even increased (Killeen & Solórzano, 2008; Chen et al., 2019). Furthemore, new protected areas considering current and future occurrences of *T. palmadora* and its pollinator are essential for its persistence and survival, as the Caatinga dry forest is currently facing high pressure from chronic anthropogenic disturbances and climate change.

Declaration of competing 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.

CRediT authorship contribution statement

Conceptualization: **DC-A, JLSS, OC-N, AVL**; data curation, formal analysis, and investigation: **DC-A**; methodology and writing: **DC-A, JLSS, OC-N, AVL**; funding acquisition, project administration, supervision, and validation: **AVL**.

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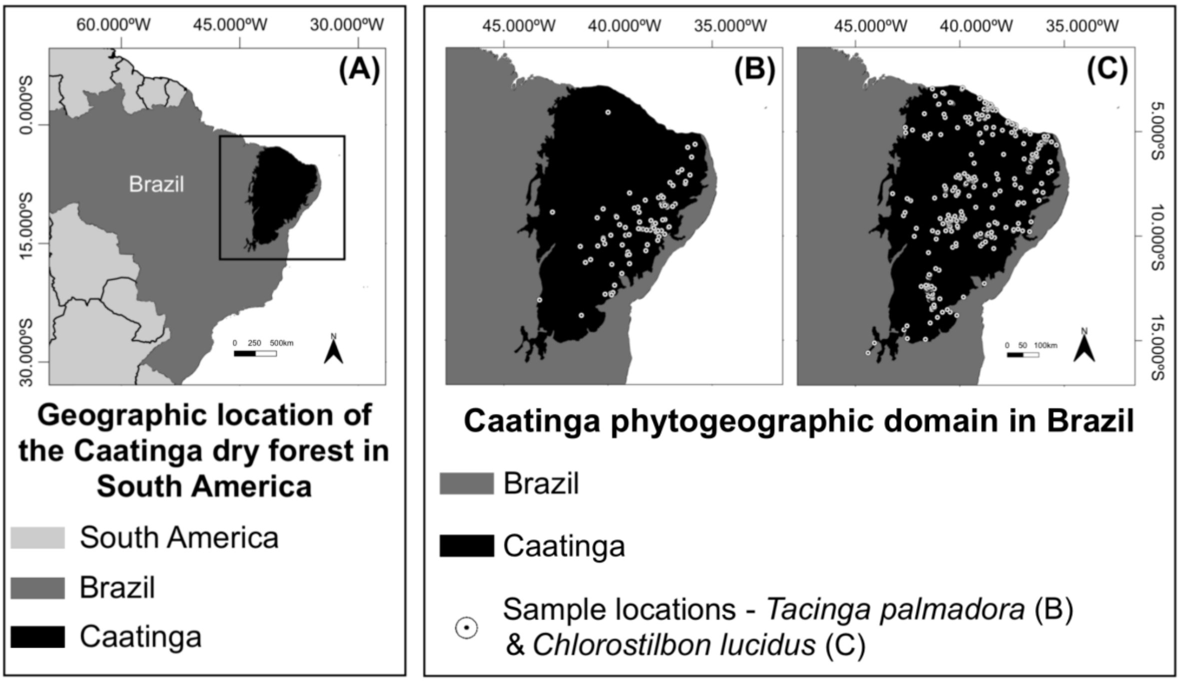

Fig. 5. Location and geographic limits of the Caatinga. Geographical location of the Caatinga dry forest in South America (A) and sampled locations in the Caatinga phytogeographic domain for plant (B) and pollinator (C). Source of the shapefiles: MMA-Ministério do Meio Ambiente, Brazil (public domain) (available for download at http://mapas.mma.gov.br/i3geo/datadownload.htm and http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm?/caatinga/dados/shape_file/).

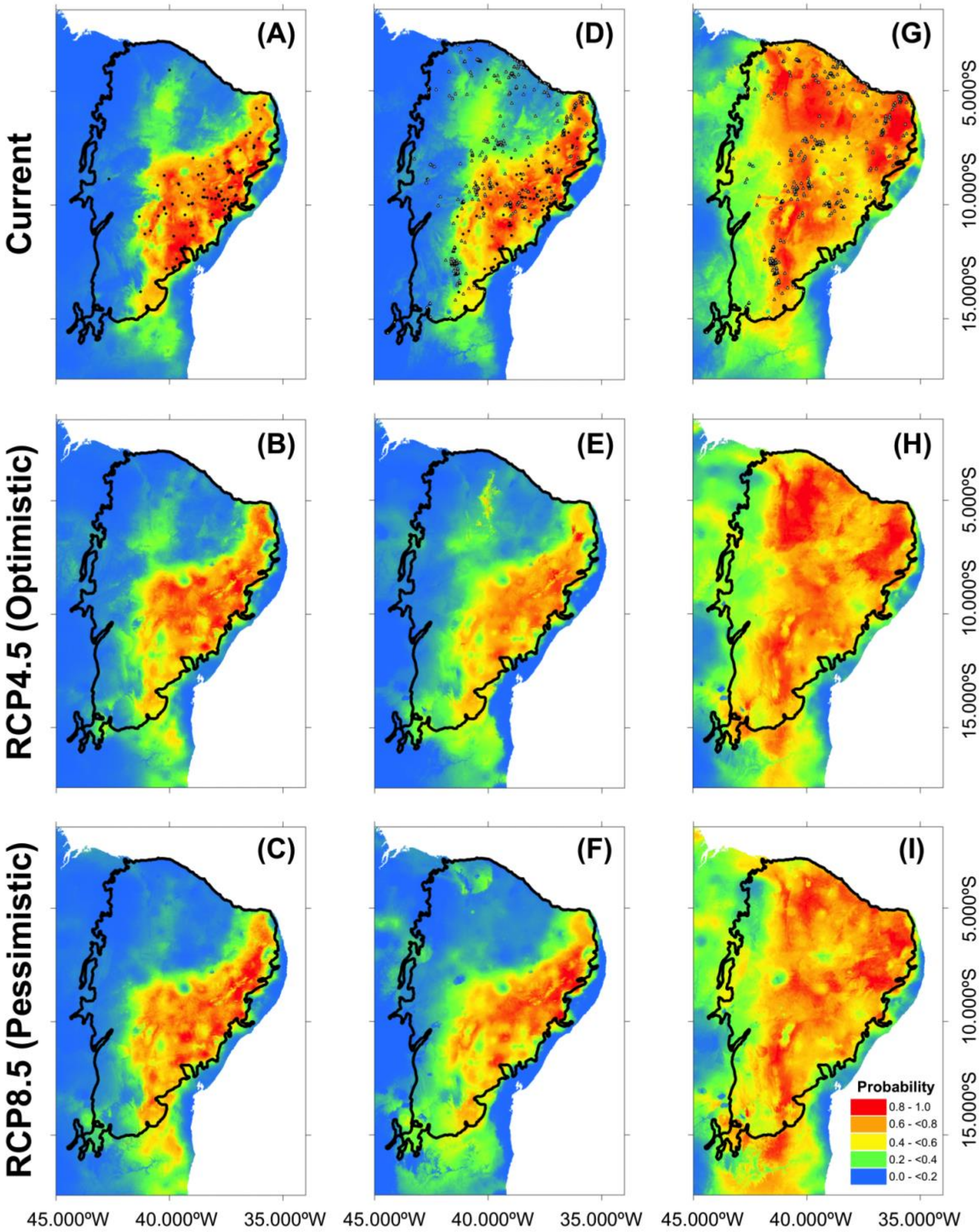

Fig. 6. Distribution of suitable habitat for *Tacinga palmadora*, using climatic variables only (A, B and C) or climatic variables and pollinator interactions (D, E and F), and its pollinator *Chlorostilbon lucidus*, using climatic variables only (G, H and I) in the Caatinga dry forest, in the present and two future scenarios, between 2070 and 2099, including an optimistic (RCP4.5) and a pessimistic (RCP8.5). Solid black dots in A and

D indicate locations of the sampled individuals of *T. palmadora*. Solid white triangles in D and G indicate locations of the sampled individuals of *C. lucidus*. Source of the shapes of the Brazilian and Caatinga boundaries: MMA-Ministério do Meio Ambiente, Brazil (public domain) (available for download at http://mapas.mma.gov.br/i3geo/datadownload.htm and http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm?/caatinga/dados/shape_file/).

Table 5. Percent contribution of the variables to the Maxent models of *Tacinga palmadora* (using climatic variables only and climatic variables and pollinator interactions) and its main effective pollinator (*Chlorostilbon lucidus*) in the Caatinga dry forest for the current period (1970–2000) and two future scenarios (2070–2099), an optimist (RCP4.5) and a more pessimist (RCP8.5).

Variable	**Percent contribution**								
	Current			**RCP4.5**			**RCP8.5**		
	T. palmadora		***C. lucidus***	***T. palmadora***		***C. lucidus***	***T. palmadora***		***C. lucidus***
	Climatic variables only	**Climatic variables + pollinator interactions**		**Climatic variables only**	**Climatic variables + pollinator interactions**		**Climatic variables only**	**Climatic variables + pollinator interactions**	
Annual Mean Temperature (BIO1)	2.0	2.6	1.2	2.9	1.7	1.7	2.9	0.7	1.6
Isothermality (BIO3)	49.1	0.7	50.9	45.2	2.0	48.3	45.0	0.7	54.2
Temperature Seasonality (BIO4)	14.0	5.0	24.3	8.3	5.6	16.1	8.3	4.0	10.4

Temperature Annual Range (BIO7)	4.3	2.4	3.4	6.5	2.6	3.4	7.9	2.5	5.7
Annual Precipitation (BIO12)	21.7	0.7	12.8	21.5	1.1	19.7	18.2	1.0	12.0
Precipitation Seasonality (BIO15)	0.3	0.7	0.3	0.2	0.4	0.4	0.7	0.4	0.4
Precipitation of Driest Quarter (BIO17)	3.9	0.3	2.3	2.8	0.4	6.1	4.3	0.2	5.7
Precipitation of Warmest Quarter (BIO18)	1.4	0.3	2.3	9.2	0.7	3.3	10.5	0.6	7.3
Precipitation of Coldest Quarter (BIO19)	3.3	0.2	2.6	3.4	0.3	0.9	2.2	0.1	5.9
Pollinator potential distribution	-	87.0	-	-	85.1	-	-	89.7	-

Table 6. Adjustments between the sampled points of *Tacinga palmadora* (using climatic variables only and climatic variables and pollinator interactions) and its main effective pollinator (*Chlorostilbon lucidus*) in the Caatinga dry forest and climatic models for the current period (1970–2000) and two future scenarios (2070–2099), an optimist (RCP4.5) and a more pessimist (RCP8.5).

Element analyzed	**Current**			**RCP4.5**			**RCP8.5**		
	AUC	**Gain**	**TSS**	**AUC**	**Gain**	**TSS**	**AUC**	**Gain**	**TSS**
	Mean ± SD			**Mean ± SD**			**Mean ± SD**		
Tacinga palmadora (Climatic variables only)	0.995 ± 0.003	4.414 ± 0.011	0.817	0.994 ± 0.003	4.299 ± 0.009	0.785	0.994 ± 0.003	4.385 ± 0.012	0.794
Tacinga palmadora (Climatic variables + pollinator interactions)	0.995 ± 0.002	4.382 ±0.008	0.819	0.994 ±0.002	4.361 ±0.009	0.816	0.994 ± 0.002	4.376 ± 0.011	0.835
Chlorostilbon lucidus (Climatic variables only)	0.977 ± 0.003	2.911 ± 0.002	0.829	0.977 ± 0.004	2.853 ± 0.003	0.748	0.976 ± 0.003	2.828 ± 0.003	0.749

Table 7. Future suitable habitats (i.e. areas with probability of occurrence > 80%) of *Tacinga palmadora* (using climatic variables only and climatic variables and pollinator interactions) and its main effective pollinator (*Chlorostilbon lucidus*) in the Caatinga dry forest in two scenarios of climate change: An optimistic (RCP4.5) and a more pessimistic (RCP8.5).

	Area of suitable habitat (km^2)					**Test**	**p**
Element analyzed	**Current**	**RCP4.5**		**RCP8.5**			
	Mean ± SD	**Mean ± SD**	**% of loss or gain***	**Mean ± SD**	**% of loss or gain***		
Tacinga palmadora (Climatic variables only)	43584.4 ± 2908.5	49901.6 ± 2503.6	12.66↑	52397.0 ± 2247.9	16.82↑	H = 63.71	<0.001
Tacinga palmadora (Climatic variables + pollinator interactions)	35651.6 ± 2631.2	24060.8 ± 2361.2	32.51↓	32690.7 ± 1692.4	8.31↓	H = 69.22	<0.001
Chlorostilbon lucidus (Climatic variables only)	140723.8 ± 2476.5	165514.3 ± 3501.5	14.98↑	143509.9 ± 2320.5	1.94↑	H = 67.33	<0.001

Appendix A supplementary information

Table 8. Georeferenced data for *Tacinga palmadora* (Cactaceae) in the Caatinga dry forest

Longitude	Latitude
-36.879167	-8.575
-37.166667	-8.616667
-37.573417	-8.163056
-39.168333	-9.594722
-37.024167	-7.440833
-36.881389	-7.583333
-38.964722	-7.940833
-38.507242	-8.864908
-37.437325	-8.481731
-38.955	-11.334722
-39.155556	-9.971111
-38.335	-9.674619
-37.432989	-9.749653
-36.77554313	-8.469940492
-38.9797	-10.8953
-39.998611	-4.068889
-37.843278	-9.531361
-38.210278	-8.285833
-35.819167	-5.604167
-36.173611	-5.749722
-37.0924	-9.5904
-37.936147	-9.261356
-40.491667	-10.482222
-36.879167	-8.575
-37.166667	-8.616667
-35.985555	-6.218611
-37.268056	-9.217222
-37.196837	-8.531343
-37.232884	-8.558099

-37.325939	-8.465799
-37.317409	-8.413305
-37.304636	-8.427781
-37.317409	-8.413305
-37.304636	-8.427781
-37.224777	-8.516704
-37.230109	-8.535398
-37.299343	-8.449588
-37.196837	-8.531343
-37.299343	-8.449588
-37.196837	-8.531343
-37.299343	-8.449588
-37.196837	-8.531343
-37.299343	-8.449588
-37.397336	-8.555353
-38.1106	-10.4211
-39.443611	-9.459444
-37.936147	-9.261356
-39.336944	-11.802778
-40.491667	-10.482222
-39.043383	-10.770114
-35.985556	-6.218611
-39.745833	-12.716111
-39.776389	-12.7275
-42.668056	-8.859722
-39.608611	-9.059444
-39.066667	-10.916667
-39.584444	-9.098056
-39.443611	-9.459444
-41.085	-11.273333
-38.145556	-9.714167
-41.331389	-10.505833
-39.018056	-9.945
-37.268056	-9.217222

-39.859167	-12.754722
-38.467222	-9.661667
-38.537222	-9.653333
-40.228611	-10.105833
-40.2275	-10.175556
-40.156389	-10.379722
-39.761111	-12.717778
-38.483333	-9.333333
-38.978056	-10.8925
-37.432778	-8.075833
-37.346944	-8.156944
-38.564722	-8.623333
-41.085556	-11.272778
-38.986944	-9.922778
-39.833333	-12.833333
-40.139722	-12.799167
-43.288056	-13.072778
-41.278056	-13.813889
-39.683333	-12.366667
-39.816667	-11.366667
-37.266667	-8.503889
-37.246944	-8.548333
-37.2575	-8.533333
-38.733333	-8.666667
-38.483333	-9.333333
-39.316667	-10.433333
-40.491667	-10.482222
-43.288056	-13.072778
-40.836111	-11.135278
-39.816667	-11.366667
-39.866667	-9.966667
-36.629167	-6.941944
-36.45475	-6.824917
-37.266667	-8.503889

-36.061111	-7.076944
-36.287222	-7.489167
-36.272222	-7.390833
-36.061111	-7.076944
-36.272222	-7.390833
-37.064299	-9.564646
-37.684167	-9.805278
-37.549722	-10.033333
-37.278056	-9.917222
-37.967444	-9.723972
-38.183333	-10.708333
-41.278056	-13.813889
-37.684167	-9.805278
-40.2275	-10.175556
-36.896111	-8.587083
-37.266667	-8.503889
-37.246944	-8.548333
-37.2575	-8.533333
-37.843111	-9.607639
-41.278056	-13.813889
-40.519722	-9.130556
-40.234756	-8.702844
-37.611703	-10.2135
-37.432989	-9.749653
-37.374189	-9.230447
-37.432989	-9.749653
-37.720647	-9.3935
-37.374189	-9.230447
-37.599656	-9.749653
-37.795419	-9.622067
-37.720675	-9.3935
-37.2575	-8.533333
-38.145556	-9.714167
-39.316667	-10.433333

-38.988056	-9.942778
-38.966667	-11.333333

Table 9. Georeferenced data for *Chlorostilbon lucidus* (Trochilidae) in the Caatinga dry forest

Longitude	**Latitude**
-44.395752	-15.583356
-44.090445	-15.107088
-41.6496	-14.9336
-42.52	-14.9
-42.5164	-14.8956
-42.675319	-14.477234
-42.5581	-14.3236
-42.540913	-14.308148
-42.532633	-14.289367
-41.422343	-14.148736
-41.07512	-13.883314
-40.147732	-13.786455
-40.836386	-13.637113
-40.465146	-13.631195
-40.599604	-13.512975
-41.3469	-13.50547
-41.346813	-13.505344
-41.337784	-13.436137
-41.221031	-13.427946
-41.23751	-13.409449
-41.243459	-13.405797
-41.218793	-13.376969
-41.239931	-13.292755
-41.451449	-13.042484
-41.365718	-13.020022
-41.374383	-13.015095

-41.40793	-13.01176
-41.371637	-13.007944
-41.370874	-13.007105
-41.366393	-13.006245
-41.369537	-13.006124
-41.400784	-12.999359
-40.956345	-12.996529
-41.386244	-12.994695
-41.355519	-12.990932
-41.348663	-12.989403
-41.348923	-12.988908
-41.34909	-12.988512
-41.35078	-12.98279
-41.34363	-12.979303
-41.286106	-12.975871
-41.327949	-12.965918
-41.329536	-12.965583
-41.312748	-12.964117
-41.315491	-12.961975
-39.828566	-12.911803
-41.31413	-12.896234
-41.505922	-12.872395
-41.33	-12.81
-41.331389	-12.807222
-41.31333	-12.765253
-41.421204	-12.744837
-41.5657	-12.638995
-41.4556	-12.600512
-41.392238	-12.581405
-41.582452	-12.576881
-41.417175	-12.576366
-41.390967	-12.574617
-41.396527	-12.571402
-41.389662	-12.569174

-41.389449	-12.568662
-41.390411	-12.566242
-41.394765	-12.564963
-41.391093	-12.561854
-41.389563	-12.561289
-41.390428	-12.561025
-41.387392	-12.560501
-41.386705	-12.560289
-41.348247	-12.557496
-41.391699	-12.556302
-41.390734	-12.556176
-41.390682	-12.554882
-41.604845	-12.554603
-41.579002	-12.55439
-41.381933	-12.554255
-41.390225	-12.551392
-41.361851	-12.550768
-41.399746	-12.550009
-41.361633	-12.547797
-41.57547	-12.54488
-41.381536	-12.543523
-41.575249	-12.543419
-41.377945	-12.542605
-41.575339	-12.541651
-41.563468	-12.540237
-41.416097	-12.540069
-41.426135	-12.534772
-41.357689	-12.532445
-41.459039	-12.531591
-41.5757	-12.5304
-41.368332	-12.529094
-41.582565	-12.523731
-41.580419	-12.514553
-41.223265	-12.513359

-41.449258	-12.482999
-41.451944	-12.478605
-41.448197	-12.477224
-41.454853	-12.474724
-41.45678	-12.471442
-41.455089	-12.470983
-41.441556	-12.469717
-41.374683	-12.468837
-41.419366	-12.462324
-41.466006	-12.457712
-41.473013	-12.45732
-41.473716	-12.456033
-41.616211	-12.45468
-41.496735	-12.437582
-41.851559	-12.404473
-41.357	-12.4029
-41.541345	-12.350483
-41.620116	-12.349141
-38.830666	-12.263523
-41.513879	-12.022465
-41.518446	-12.022011
-41.521926	-12.018718
-41.521876	-12.016596
-41.527082	-12.013274
-41.525071	-12.012745
-41.526022	-12.011006
-41.4928	-12.005712
-41.525244	-11.986065
-41.524649	-11.985453
-41.523557	-11.982317
-41.522602	-11.978782
-41.522247	-11.976914
-41.519262	-11.970961
-41.518726	-11.969693

-41.510999	-11.957849
-41.463952	-11.89067
-41.461416	-11.885949
-41.459912	-11.884278
-41.454279	-11.878394
-41.465453	-11.859052
-41.433052	-11.848149
-41.469589	-11.839415
-40.9996	-11.625214
-41.153412	-11.558744
-41.156111	-11.55
-41.505737	-10.786733
-38.379695	-10.590478
-40.347673	-10.531322
-40.181122	-10.464126
-39.007322	-10.463421
-38.916338	-10.367234
-40.186105	-10.3486
-38.777502	-10.269874
-41.141454	-10.147798
-41.133649	-10.137856
-38.445368	-10.09178
-38.390038	-10.091016
-38.99098	-10.081867
-38.46192	-10.075365
-38.346705	-10.071967
-38.342285	-10.069435
-38.996516	-10.06493
-38.479623	-10.064621
-38.480798	-10.063721
-38.485124	-10.054211
-38.997986	-10.045301
-38.99613	-10.04471
-38.994929	-10.030571

-38.481674	-10.027681
-39.00131	-10.01682
-39.240417	-10.010777
-42.182688	-10.006809
-39.155273	-9.960735
-38.995685	-9.956302
-38.99581	-9.95624
-38.707224	-9.954161
-39.015983	-9.945035
-39.016018	-9.944983
-39.015936	-9.944967
-39.015916	-9.944845
-39.020476	-9.944081
-39.032976	-9.927716
-39.05365	-9.92286
-39.147377	-9.92189
-38.687117	-9.905963
-39.02819	-9.896182
-41.106698	-9.895722
-41.10711	-9.895613
-39.034188	-9.89238
-41.126905	-9.89237
-41.126356	-9.890517
-41.127204	-9.890198
-41.125767	-9.890143
-41.122846	-9.889641
-41.12698	-9.888932
-41.09616	-9.888394
-41.126712	-9.887505
-41.098242	-9.887486
-41.126589	-9.886724
-41.100015	-9.886401
-41.100171	-9.88617
-41.126533	-9.885875

-41.107332	-9.883371
-39.008218	-9.876442
-38.637736	-9.873735
-38.642403	-9.872367
-41.100437	-9.864053
-41.070304	-9.863373
-41.108309	-9.858875
-41.108345	-9.858814
-41.109785	-9.857567
-41.110392	-9.85674
-41.111293	-9.855615
-41.113328	-9.852469
-41.113099	-9.851079
-41.112582	-9.850048
-41.112521	-9.849793
-41.082006	-9.846825
-41.111062	-9.846059
-41.081064	-9.844943
-41.080361	-9.843225
-41.081146	-9.837837
-41.082113	-9.832928
-41.053447	-9.820786
-38.489957	-9.811324
-36.662045	-9.780302
-40.401944	-9.761111
-36.998183	-9.744388
-37.431799	-9.743298
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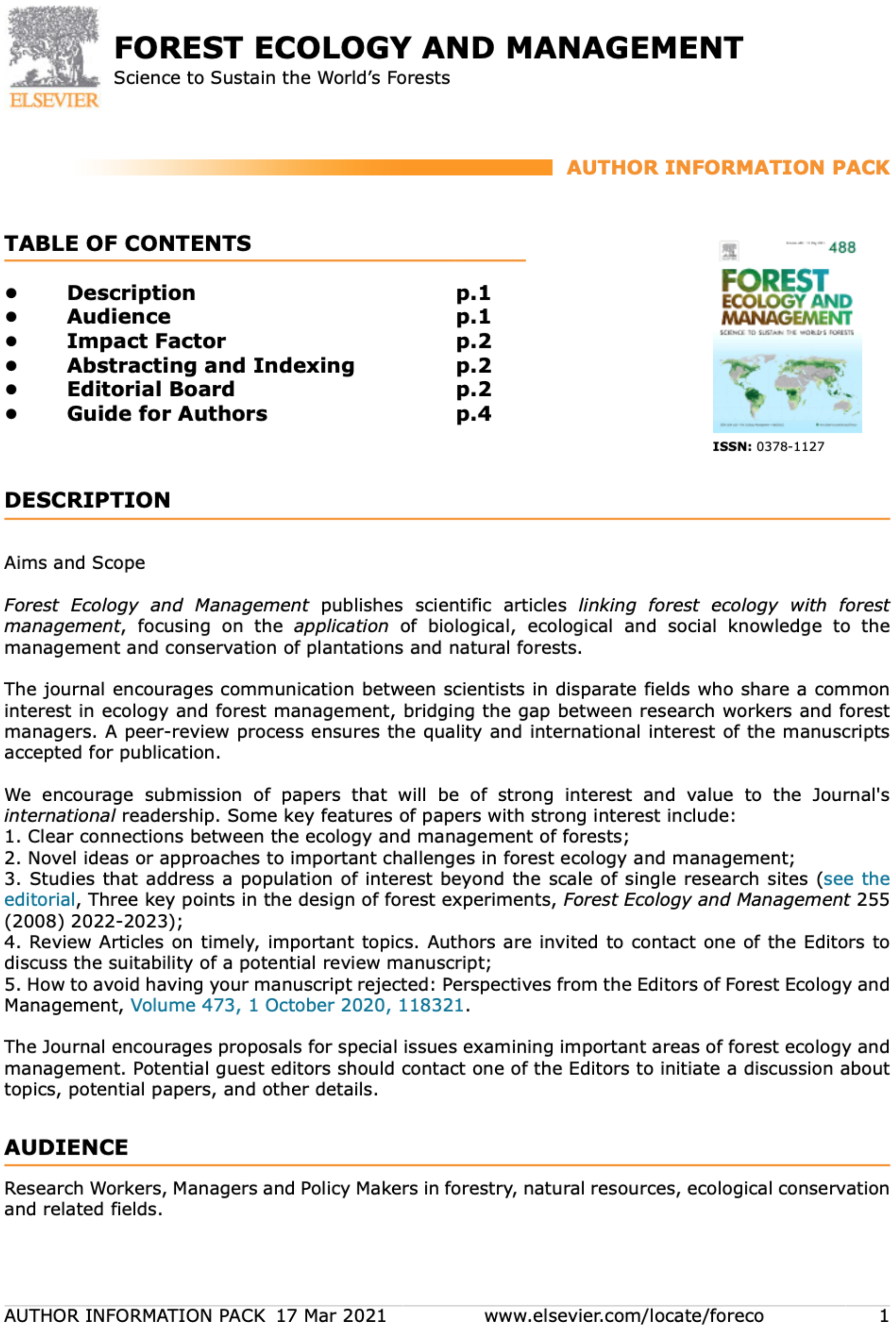
6 CONCLUSIONS

Results from the first chapter revealed that reductions of *Tacinga palmadora* pollen traits (number of pollen grains, pollen viability and pollen-ovule ratio) are associated with increasing chronic anthropogenic disturbance (CAD) and aridity, and increases in fruit- and seed-set, both by open pollination, are associated with increasing aridity and CAD, respectively. On the other hand, the fruit- and seed-set by spontaneous self-pollination are maintained under the influence of increasing CAD and aridity. Therefore, even though the pollen traits evaluated are reduced by higher CAD and aridity, pollination of *T. palmadora* is maintained or even increased in the most disturbed and arid areas of Catimbau NP, thus pollination efficiency in its populations might be currently adapted to disturbance and aridity in the Caatinga forest.

On the contrary, results from the second chapter revealed that the models that include pollinator interactions explain better the potential distribution of *T. palmadora*. Furthermore, the plant species is vulnerable to future climate change and may lose a part of its climatic envelope, in relation to climatic variables and pollination interaction. Thus, although the species is not currently vulnerable to chronic anthropogenic disturbances and climate change, in the long term it will most likely be vulnerable and conservation strategies for both the plant species and the pollinator are important. Considering the high pressures from disturbances and climate change in the Caatinga dry forest, new protected areas considering current and future occurrences of *T. palmadora* and its pollinator are essential for the plant species persistence and survival.

7 APPENDICES

7.1 APPENDIX A - STANDARDS FOR PUBLICATION IN THE JOURNAL “FOREST ECOLOGY AND MANAGEMENT”



FOREST ECOLOGY AND MANAGEMENT
Science to Sustain the World’s Forests
ELSEVIER

AUTHOR INFORMATION PACK

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ISSN: 0378-1127

DESCRIPTION

Aims and Scope

Forest Ecology and Management publishes scientific articles *linking forest ecology with forest management*, focusing on the *application* of biological, ecological and social knowledge to the management and conservation of plantations and natural forests.

The journal encourages communication between scientists in disparate fields who share a common interest in ecology and forest management, bridging the gap between research workers and forest managers. A peer-review process ensures the quality and international interest of the manuscripts accepted for publication.

We encourage submission of papers that will be of strong interest and value to the Journal's *international* readership. Some key features of papers with strong interest include:
1. Clear connections between the ecology and management of forests;
2. Novel ideas or approaches to important challenges in forest ecology and management;
3. Studies that address a population of interest beyond the scale of single research sites (see the editorial, Three key points in the design of forest experiments, *Forest Ecology and Management* 255 (2008) 2022-2023);
4. Review Articles on timely, important topics. Authors are invited to contact one of the Editors to discuss the suitability of a potential review manuscript;
5. How to avoid having your manuscript rejected: Perspectives from the Editors of Forest Ecology and Management, Volume 473, 1 October 2020, 118321.

The Journal encourages proposals for special issues examining important areas of forest ecology and management. Potential guest editors should contact one of the Editors to initiate a discussion about topics, potential papers, and other details.

AUDIENCE

Research Workers, Managers and Policy Makers in forestry, natural resources, ecological conservation and related fields.

7.2 APPENDIX B – STANDARDS FOR PUBLICATION IN THE JOURNAL “BIOLOGICAL CONSERVATION”

BIOLOGICAL CONSERVATION

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ISSN: 0006-3207

DESCRIPTION

Biological Conservation is a leading international journal in the discipline of **conservation science**. The journal publishes articles spanning a diverse range of fields that contribute to the biological, sociological, ethical and economic dimensions of **conservation**. The primary aim of *Biological Conservation* is the publication of high-quality papers that advance the science and practice of conservation, or which demonstrate the application of conservation principles and policy. *Biological Conservation* invites the submission of research articles, reviews (including systematic reviews and perspectives), short communications, policy perspectives, and letters to the editor dealing with all aspects of conservation science, including theoretical and empirical investigations into the consequences of human actions for the diversity, structure and function of terrestrial, aquatic or marine ecosystems. Such papers may include quantitative assessments of extinction risk, fragmentation effects, spread of invasive organisms, conservation genetics, conservation management, global change effects on biodiversity, landscape or reserve design and management, restoration ecology, or resource economics. We also welcome papers coming from social sciences including those reporting on advances in conservation politics, ethics, policy, human social structure and biodiversity, and political culture among other subjects. *Biological Conservation* covers interdisciplinary topics within conservation biology and also provides practical applications of conservation research for land/resource managers and policy makers. We publish articles and thematic special issues that have a global relevance in terms of the topics or issues addressed, and thus demonstrate applications of conservation science and management beyond the specific system or species studied.Biological Conservation is an affiliate publication of the Society for Conservation Biology (SCB). SCB members can obtain a personal subscription to this journal through the Society. Authors are also welcome to submit to the Journal?s open access companion title, *Global Ecology and Conservation*, which covers all sub-disciplines of ecological and conservation science.

AUDIENCE

Environmentalists, conservationists, botanists, marine scientists, ecologists, biologists, zoologists.

IMPACT FACTOR

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