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ORIGINAL PAPER

Climate projections and the future of invasive plants in the Caatinga

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Abstract The increasing prevalence of invasive plants thriving under changing climates underscores a major ecological concern. While many studies address invasions at broad taxonomic scales, our approach emphasizes the simultaneous projection of multiple species grouped by functional traits. In addition to modeling their joint distribution, we evaluated the persistence and spatial overlap between functionally distinct invaders as a possible indicator of future ecological shifts. Ecosystems like the Brazilian Caatinga, a seasonally dry tropical forest spanning 833,000 km^2, may be especially vulnerable to invasions and climate change due to widespread land degradation. We projected the future distribution of 11 invasive species under both optimistic and pessimistic climate scenarios, spanning 2021 to 2100. Potential distribution changes were assessed considering the joint invasion of all species, grouped into woody and non-woody categories. Areas with annual mean temperatures between 24 and 27 °C and higher precipitation were more prone to invasions. Non-woody species are projected to occupy the largest high-suitability areas throughout the century. *Cenchrus ciliaris* L. and *Prosopis juliflora* (Sw.) are examples of major invaders under both scenarios. One region in the Caatinga remained suitable for both woody and non-woody invaders, reflecting a localized zone of functional co-occurrence retention despite overall habitat contraction. Even with projected declines in suitable areas (−36.4% optimistic, −28.2% pessimistic), the continued presence of invasive species poses risks to native flora, which is generally more sensitive

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to environmental change. These results highlight the urgency of proactive management to safeguard biodiversity.

Keywords Seasonally dry tropical forest (SDTF) · Invasive plant species · Climate change · Species distribution model (SDM) · Co-occurrence patterns

Introduction

Biological invasions, driven largely by human-mediated species introductions, are among the main causes of global biodiversity loss. Some non-native species display high adaptability to novel environments due to intrinsic traits such as rapid growth, efficient reproduction, and high dispersal capacity (Marin et al. 2020; Pinto et al. 2020). While many of these species can become established and persist in new habitats, only a subset is classified as invasive, meaning they not only spread widely but also cause significant negative impacts on native biodiversity, ecosystem functioning, or human well-being. Once established, invasive species can outcompete native flora, disrupt ecological processes, and alter physicochemical conditions, especially where multiple invaders co-occur (Diagne et al. 2021; Pérez et al. 2022; Xu Yue et al. 2016). Their presence threatens biodiversity and ecosystem services critical to human well-being, including food production, medicinal resources, and environmental regulation (Pejchar and Mooney 2009; Jones and McDermott 2018). Additionally, they can cause substantial economic losses, particularly in agriculture and livestock sectors (Essl et al. 2020; Gaertner et al. 2014), and pose growing risks to human health (Pyšek and Richardson 2010; Stone et al. 2018).

Understanding the variety of impacts caused by invasive plants requires consideration of their functional differences, as these traits influence how species interact with ecosystems, respond to disturbances, and compete for resources (Díaz et al. 2016; Weigelt et al. 2021). Functional traits, such as growth form, rooting depth, reproductive strategy, and dispersal mechanisms, are key predictors of invasion success and ecological impact (Díaz et al. 2016; Funk et al. 2008; Weigelt et al. 2021). Grouping species by functional characteristics allows researchers to generalize patterns and better assess the risks posed by different types of invaders (Catford et al. 2009; Díaz et al. 2016; Funk et al. 2008; Weigelt et al. 2021).

These functional distinctions are also relevant when considering the spatial co-occurrence of invasive species under climate change (Díaz et al. 2016; Weigelt et al. 2021). When species from different functional groups are projected to persist in the same regions, they may form or reinforce co-occurrence patterns that appear to be relatively recent, involving combinations of invasive species that, although already observed in some areas, may have emerged only in recent decades as a result of ongoing invasion processes. These zones of overlapping habitat suitability can be ecologically significant, as the coexistence of functionally distinct invaders may alter competitive dynamics, resource availability, and disturbance regimes in ways that differ from existing native community structures (Fastovich et al. 2020; Feeley et al. 2020; Williams and Jackson 2007). This line of thinking is inspired by the concept of no-analog communities, assemblages without historical precedent in terms of species composition or ecological function, although such patterns may already be taking shape and simply have received limited attention so far (Williams and Jackson 2007; Blois et al. 2013).

Beyond co-occurrence patterns, understanding the individual responses of invasive plant species to environmental pressures, such as their capacity to establish and spread, is also crucial (Blois et al. 2013; Rejmánek and Richardson 2013). These responses are shaped by factors ranging from intentional introductions to climate change (Chagas et al. 2020; Gioria et al. 2023). Climate change, in particular, has disrupted the natural conditions across much of the planet, leading to ongoing shifts in the distribution of species. However, regional susceptibility to climate-driven invasions is not uniform and can be shaped by factors such as historical land degradation, which compromises native vegetation and reduces ecosystem resilience (Hansen and Cramer 2015; Knoke et al. 2023). Seasonally dry tropical forests (SDTF) worldwide have experienced notable environmental degradation, partially reflecting a historical disregard that often perceives these ecosystems as less productive and diverse (Ferrer-Paris et al. 2019; Rivas et al. 2021). Simultaneously, these regions are expected to undergo severe changes in precipitation and temperature (Marengo et al. 2020; Seddon et al. 2016).

As a result, there are questions about the potential for biological invasions in such environments, including whether the extreme climatic conditions anticipated in SDTFs would promote or deter invasive species (Chagas et al. 2020).

One way to approach this question is by examining specific SDTFs, which present unique challenges due to their pronounced seasonality and ecological heterogeneity. SDTFs are not defined by a single set of universally applicable criteria, which makes it difficult to generalize invasion dynamics across regions. This can result in significant differences in biological invasions from one place to another (Maass and Burgos 2011; Meir and Pennington 2011; Pinto et al. 2020). One unique SDTF is located in the northeastern region of Brazil, known as the Caatinga. It covers an extensive area of 833,000 km^2, which is three and a half times larger than the United Kingdom (Fernandes et al. 2020). Recognized as the most expansive SDTF, it is home to roughly 10% of Brazil's total plant diversity, with about 15% being SDTF specialists found exclusively in the Caatinga (Fernandes et al. 2020; Zappi 2015). In terms of introduced species, the Caatinga harbors over 120 species, not all of which necessarily cause severe socioeconomic or ecological harm (Almeida et al. 2015). On the other hand, 51 species are classified according to their invasion risk, including the Asian shrub *Calotropis procera* Aiton (Silk Cotton) and the Mexican tree *Leucaena leucocephala* Lam. (Leucaena) (Leão et al. 2011). These species thrive in the Caatinga due to local similarities with their native countries (Barbosa et al. 2019; Hassan et al. 2015) and affect ecosystem services, particularly those related to regulation (Jones and McDermott 2018; Leão et al. 2011; Rai and Singh 2020).

As climate change continues to reshape our planet, ecosystems like the Caatinga stand at the threshold of significant transformations (Lopes et al. 2023). With this perspective, our study is grounded in two primary objectives: (1) to identify the average suitable areas for biological invasions in the Caatinga using consensus Species Distribution Models (SDMs); and (2) to identify invasive species, broadly classified into woody and non-woody groups, that may thrive under projected climatic changes and potentially alter trophic structures and ecosystem functioning. This functional classification captures key ecological strategies, with woody species often exerting long-term structural and competitive dominance (Rejmánek and Richardson 2013; Schmidt et al. 2020), while non-woody species tend to display rapid colonization in disturbed habitats (Underwood et al. 2019; Scharfy et al. 2011), both of which are relevant for understanding invasion dynamics in seasonally dry environments. Rather than attempting to simulate full community composition or species interactions, we adopt a spatially grounded approach by identifying areas where multiple invasive species, drawn from two distinct functional groups, are projected to retain overlapping suitability under future climatic conditions. This provides an initial, ecologically meaningful indication of regions where co-occurrence patterns of invasive species may already exist, persist, expand, or contract in response to climate change. Given the size and environmental heterogeneity of the Caatinga, we hypothesize that areas with higher precipitation will be especially vulnerable, as water availability remains a primary limiting factor (Maass and Burgos 2011; Meir and Pennington 2011; Prochazka et al. 2024). Furthermore, species with high reproductive potential, often represented by non-woody invaders, may be particularly favored under future conditions, potentially expanding their geographic range and ecological influence.

Materials and method

Study area

This study focuses on the Brazilian Seasonal Dry Tropical Forest (SDTF) known as the Caatinga, which covers an area of 833,000 km^2 (Fernandes et al. 2020; IBGE, 2019a). Within this region, certain areas endure a prolonged drought period lasting six to eight months, during which precipitation is less than twice the temperature (Bagnouls and Gaussen 1953). The climate in the Caatinga is predominantly semi-arid (Vieira et al. 2015), with average annual precipitation levels around 800 mm, which can exceed 1,000 mm in coastal regions and drop to less than 300 mm in some continental areas. The rainy season in the Caatinga typically extends from January to May, although this can vary due to extreme weather events and differences in precipitation across the various vegetation strata within the ecosystem (Silva et al. 2019a, b). Throughout the year, the region experiences a range

of temperatures, generally fluctuating between 22 °C and 30 °C (Morais et al. 2021; Silva et al. 2019a, b).

This seasonal difference, along with the unique characteristics of the Caatinga as a SDTF and its proximity to the coastal Atlantic Forest, results in shared vegetative similarities among the Caatinga area. Such vegetative similarities give rise to various ecological features, including the presence of Seasonal Forests, Savanna Complexes, Dunes, and vegetation fragments influenced by hydrological factors (Silva et al. 2019a, b). In turn, these environmental characteristics shape the survival strategies developed by native plants to endure the dry months (Fernandes and Queiroz 2018; Meir and Pennington 2011; Oliveira et al. 2018). Native species in the Caatinga are already adapted to its climate, which includes the shortest rainy season (3–5 months) among all SDTFs, leading to traits such as small and leathery leaves, thorns, deep roots, and twisted trunks, as well as pronounced variation in vegetation structure, from forests to xerophytic shrublands (Fernandes and Queiroz 2018; Meir and Pennington 2011).

The Caatinga naturally challenging climate is expected to become harsher with climate change. Projections indicate a temperature increase of at least two degrees by 2040, four degrees by 2070, and an impressive five and a half degrees by 2100 (Marengo et al. 2020). These changes will have far-reaching impacts on factors such as water availability, the supply of animal feed, and local agricultural production. They are expected to contribute to the ongoing desertification process (Nolan et al. 2018; Ringelberg et al. 2023) and significantly affect the local diversity (De Kort et al. 2021; Fontúrbel et al. 2018).

Species distribution models (SDMs)

Predicting the invasibility of ecosystems such as the Caatinga requires tools capable of estimating potential changes in species distributions under future climatic scenarios. Species Distribution Models (SDMs) offer an approach to this task by correlating georeferenced occurrence data with environmental variables, such as climate, soil, and topography (Chagas et al. 2020; Lin et al. 2023). Through this modeling, it is possible to identify areas of higher suitability for non-native and invasive non-native species, supporting management efforts and ecological planning (Essl et al. 2020; Silva et al. 2019a, b).

The Maximum Entropy (MaxEnt) machine learning algorithm was used to construct SDMs for species that are invasive in the Caatinga. SDMs are predicated on the ecological niche concept, representing the range of conditions and resources necessary to sustain populations within an ecosystem (Polechová and Storch 2008). The primary output of SDMs is habitat suitability maps reflecting the environmental conditions essential for a species existence or survival (Ganglo 2023; Sun et al. 2022).

MaxEnt employs the maximum entropy principle to estimate the *relative occurrence rate* of a species across a landscape, based on environmental predictors at each location. In physics, this approach corresponds to a measure of uncertainty in the state of a system, and in the context of MaxEnt, it is used to predict where a species might exist based on available data (Baldwin 2009; Merow et al. 2013). The relative occurrence rates predicted by MaxEnt, denoted as $P^*(z)$, are calculated using the formula:

$$P*(z) = Q(z)\exp(\lambda \cdot z)/\Sigma_z Q(z')\ \exp\left(A \cdot z'\right)$$

In this equation, z is the vector of environmental variables at a location, λ is the vector of feature weights (regression coefficients), and (z) represents the empirical distribution of background environmental conditions, which incorporates sampling bias through the use of a bias file. The numerator captures how well the environmental conditions at a given location align with those associated with known species occurrences, while the denominator ensures normalization across the landscape (Merow et al. 2013).

The model assigns a predicted suitability score to each cell within the study area, reflecting the necessary conditions for the species survival. These scores do not represent true probabilities of presence but rather indices of habitat suitability that can be interpreted as the species' relative preference across the landscape (Ganglo 2023; Merow et al. 2013).

The results obtained through modeling should be interpreted with caution, especially in studies involving multiple populations of species. Information about these populations may be scarce, such as their health and their ecological interactions with the environment. These factors are important for constructing specific environmental predictors, which could potentially improve the accuracy of distribution models, despite the availability of

high-quality, non-customized predictors on the internet (Booth 2022; Ganglo 2023; Hui 2023).

Climate change scenarios

Climate change scenarios, providing insights into future climate conditions, are developed based on factors such as greenhouse gas emissions and other relevant variables (Joshi et al. 2003; Kärcher 2018). These scenarios represent possible futures and can already be tailored to specific Global Climate Models (GCMs), which are computer models used to simulate the Earth's climate system (Braconnot et al. 2012; Kirtman et al. 2013). In this study, future climate data from the WorldClim database (https://www.worldclim.org) were used, which incorporates a range of these climate scenarios associated with different GCMs. These scenarios consider diverse emissions, socioeconomic developments, and other relevant factors that align with the respective GCMs, allowing for the exploration of a spectrum of potential climate outcomes (Keyßer and Lenzen 2021; Riahi et al. 2017).

The GCM used in this study was the EC-Earth3-Veg, in which the study area exhibits some climatic characteristics similar to those of the semi-arid region, in addition to being an efficient model for representing the effects of climate change on vegetation with greater accuracy. Only one GCM was used to facilitate modeling with more than two species (Abbas et al. 2022; Lin et al. 2023; Parding et al. 2020), and associated with it, an optimistic (ssp1-2.6) and a pessimistic (ssp5-8.5) scenario were used. In the optimistic scenario, a world with low greenhouse gas emissions (2.6 watts per square meter of radiative forcing until 2100) is simulated, with the aim of limiting global warming to less than 2 degrees Celsius above pre-industrial levels (O'Neill et al. 2016). In contrast, the pessimistic scenario simulates a trajectory marked by global population growth and a heavy reliance on fossil fuels as the basis of the world economy. This leads to a substantial increase in greenhouse gas emissions (8.5 watts per square meter of radiative forcing in 2100), resulting in a significant increase in global average temperatures from 4.1 to 4.8 °C above pre-industrial levels by 2100 (Brooks et al. 2014; O'Neill et al. 2016).

Data collection

A total of 22 monthly variables were collected based on their relevance as factors for predicting species' future distribution, as indicated in the literature (Ganglo 2023). These variables were obtained at a five-minute spatial resolution (in minutes of longitude and latitude) for four future time intervals (2021–2040, 2041–2060, 2061–2080, and 2081–2100). A detailed list and description of all variables is provided in Appendix A.

A previous study identified 51 invasive species in the Caatinga based on their established presence in natural environments, their recognition as invaders in the region, and their occurrence in at least three of the ten states within the Caatinga's boundaries (Leão et al. 2011). The occurrences for these invasive species were extracted from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and SpeciesLink (https://specieslink.net/). To minimize potential errors commonly associated with GBIF data, such as imprecise coordinates or records from cultivated individuals, we restricted the data to records from peer-reviewed publications and herbarium specimens only. We also removed duplicates and excluded records without geographic coordinates or with clearly erroneous spatial information (Moudrý et al. 2024; Xu et al 2022; Zizka et al. 2019).

To enhance model robustness, only species with at least 100 georeferenced occurrences within the Caatinga were selected. Additionally, species cultivated for multiple purposes were excluded to avoid modeling issues related to immature or unstable populations, such as economic use, horticulture, medicine, food, or ornamental purposes. Cultivated plants are often managed in ways that do not reflect natural conditions and may include young or recently planted individuals that are not fully established. By excluding such species, we ensure that our data reflects populations that are more likely to be mature and stable, rather than those potentially subject to frequent disturbances or economic exploitation (Brinckmann et al. 2022; Xia et al. 2022). This approach is supported by information from the Brazilian database Instituto Horus (https://bd.institutohorus.org.br/). These criteria led to the selection of 11 of the 51 species listed in the literature.

Occurrences from both the species' native and invaded ranges were included to refine the modeling

outcomes (Bergamin et al. 2022; Broennimann and Guisan 2008). For each species, up to 1500 occurrence points were selected from each range and used together in the modeling process (Supplementary 1). Furthermore, the species were classified into two broad functional groups based on their structural characteristics: woody species, comprising perennial plants with developed woody tissues such as trees and shrubs, and non-woody species, consisting of herbaceous plants like forbs and grasses, typically characterized by rapid growth and flexible rooting systems (Rejmánek and Richardson 2013; Scharfy et al. 2011).

The modeling of the distribution of invasive plant species was designed to provide a broad understanding of potential impacts of future climate changes. We opted not to include species-specific factors such as dispersal mechanisms, ecological interactions, or disturbance responses in the model. This approach enhances the comparability and reproducibility of the study, as it relies on standardized and widely accessible data. This strategic focus provides preliminary insights into the potential distributional shifts of invasive species under changing climatic conditions, facilitating broader ecological and conservation planning efforts (Booth et al. 2014).

Statistical approach

A pairwise correlation analysis of the 22 variables was conducted to minimize multicollinearity and enhance modeling accuracy. Pairs of variables with a Pearson correlation coefficient of $r \geq 0.8$ or $r \leq -0.8$ ($|r| \geq 0.8$) were considered highly correlated, and in each case, one variable was removed. Although a threshold of 0.7 is common in ecological modeling (Dormann et al. 2013), we adopted the more conservative value of 0.8 based on the moderate number of predictors and the ecological focus of the study (Dai et al. 2022; Dormann et al. 2013). This value balances the reduction of collinearity with the preservation of biologically meaningful variables, and aligns with recommendations from previous studies where fewer, ecologically grounded predictors were employed (Dormann et al. 2013; Elith et al. 2006; Graham 2003).

For each correlated pair, the retained variables were chosen based on ecological relevance to the Caatinga, functional characteristics of both woody and non-woody invasive species and the climatic dynamics of seasonally dry tropical forests, with particular attention to precipitation and temperature regimes, following guidance from the literature and expert-based reasoning (Dormann et al. 2013; Feng et al. 2019; Fernandes, Queiroz, 2018; Fernandes et al. 2020; Lin, Chiu, 2020; Maass, Burgos, 2011; Nievola et al. 2017; Ringelberg et al. 2023; Whittingham et al. 2006).

Ultimately, only seven variables were retained (Table 1), five of which were precipitation related. This predominance reflects not only the statistical outcome of the multicollinearity filtering process but also aligns with the ecological characteristics of the Caatinga, where water availability plays a central role (Alves and Fabricante 2019; Barbosa et al. 2019; Ramos et al. 2023; Ribeiro Menezes et al. 2022; Salimon and Anderson 2017). Nevertheless, temperature-related variables were also retained, possibly

Table 1 Multicollinearity test using the Pearson correlation coefficient of environmental variables. Only the variables with $r \geq 0.8$ are shown

Variable	Bio1	Bio3	Bio12	Bio15	Bio17	Bio19	pr
Bio1	1						
Bio3	0.708	1					
Bio12	−0.095	0.003	1				
Bio15	0.414	0.507	−0.034	1			
Bio17	−0.243	−0.299	0.367	−0.435	1		
Bio19	0.522	0.544	0.560	0.095	0.191	1	
Pr	0.099	0.190	0.367	−0.435	0.632	0.478	1

Bio1 = Annual mean temperature (°C), Bio3 = Isothermality (%), Bio12 = Annual precipitation (mm), Bio15 = Precipitation seasonality (mm), Bio17 = Precipitation of the driest quarter (mm), Bio19 = Precipitation of the coldest quarter (mm), Pr = Monthly total precipitation (mm)

reflecting the importance of thermal conditions in shaping species distributions in seasonally dry tropical environments (Cláudio et al. 2024; Gonçalves et al. 2017; Nievola et al. 2017).

To mitigate potential issues related to spatial autocorrelation and sampling bias in the occurrence data, we generated a bias surface based on the spatial density of occurrence points. Using the R statistical environment (R Core Team 2016), we rasterized the georeferenced occurrence records of the 11 invasive species over a global template raster constructed from the final set of seven environmental variables selected after multicollinearity reduction. We then applied a kernel density function to estimate the intensity of sampling effort across the study area, generating a continuous bias layer. This bias surface was exported in ASCII (a plain-text raster format commonly used in GIS) format and used as a sampling bias file in MaxEnt to guide background point selection and reduce overfitting (Merow et al. 2013; Senula et al. 2019; Stanley et al. 2018; Zizka et al. 2019). All steps were conducted using the raster and dismo packages in R.

The initial step in MaxEnt involved importing the seven variables and georeferenced data points. The algorithm was set to calculate linearity, quadratic, and product features of the variables to generate response curves (Merow et al. 2013). Evaluating the linearity of the data ensures, for example, that the mean precipitation in areas where the species can be found is roughly equivalent to the mean precipitation in areas where they are currently observed. Quadratic features, on the other hand, help restrict the variance in precipitation at potential species occurrence locations to match the variance in observed locations. Meanwhile, product features help ensure that the relationship between precipitation and other factors is controlled or constrained (Merow et al. 2013).

Variable contribution and model evaluation were assessed using MaxEnt's built-in procedures. The algorithm was configured to calculate the relative importance of variables through the Jackknife test, which incorporated Principal Component Analysis (PCA) (Bradie and Leunig 2017; Merow et al. 2013). The area under the curve (AUC), a discriminative metric used to distinguish between species presence and false records, was computed to validate the obtained results (Lin et al. 2023; Parding et al. 2020). The AUC values range from zero to one, with values closer to one indicating better results. These analyses were performed in MaxEnt for each of the 11 invasive species in 500 iterations, reaching convergence at 0.00001 (Martins et al. 2020; Merow et al. 2013).

All 11 species included in the analysis had AUC values ≥ 0.7, indicating reliable model performance (Fig. 1). Given this satisfactory performance, the SDMs for these 11 species were overlaid to create a consensus set of SDMs for both climate change scenarios and their four-time intervals, aiming to represent the average potential habitats that could be invaded by these species. To achieve this, the individual models were combined using the 'mean' command in the R base package (R Core Team 2016).

Classification of invasion suitability was based on the continuous values produced by the consensus maps, which range from 0 to 1 (Merow et al. 2013). Suitability levels were defined using conservative thresholds based on the strength of model predictions: low suitability was assigned to values below 0.8, medium suitability to values between 0.8 and 0.89, and high suitability to values above 0.9. These thresholds were chosen to highlight areas with the greatest potential for invasion under future climatic conditions.

Classification was performed in QGIS V.3.40.6 using raster analysis tools. The *r.report* function was applied to summarize the area (in km^2) associated with each suitability class (Kurt Menke et al. 2016). As a form of validation, polygons were manually delineated over the classified rasters, and their areas were calculated using the "Calculate Geometry" plugin in QGIS, which computes polygon area and line length in user-defined units.

Identification of functional co-occurrence zones

An exploratory spatial approach using QGIS V.3.40.6 (Senf et al. 2021) was employed to assess changes in functional co-occurrence among invasive species under future climate scenarios. Georeferenced occurrences of the 11 invasive species were kept constant for both time periods (2021–2040 and 2081–2100), allowing the analysis to focus exclusively on projected shifts in habitat suitability (Elith and Leathwick 2009; Yang et al. 2015).

Areas with high suitability (values > 0.9) projected for both woody and non-woody invasive species were identified as functional co-occurrence zones. These

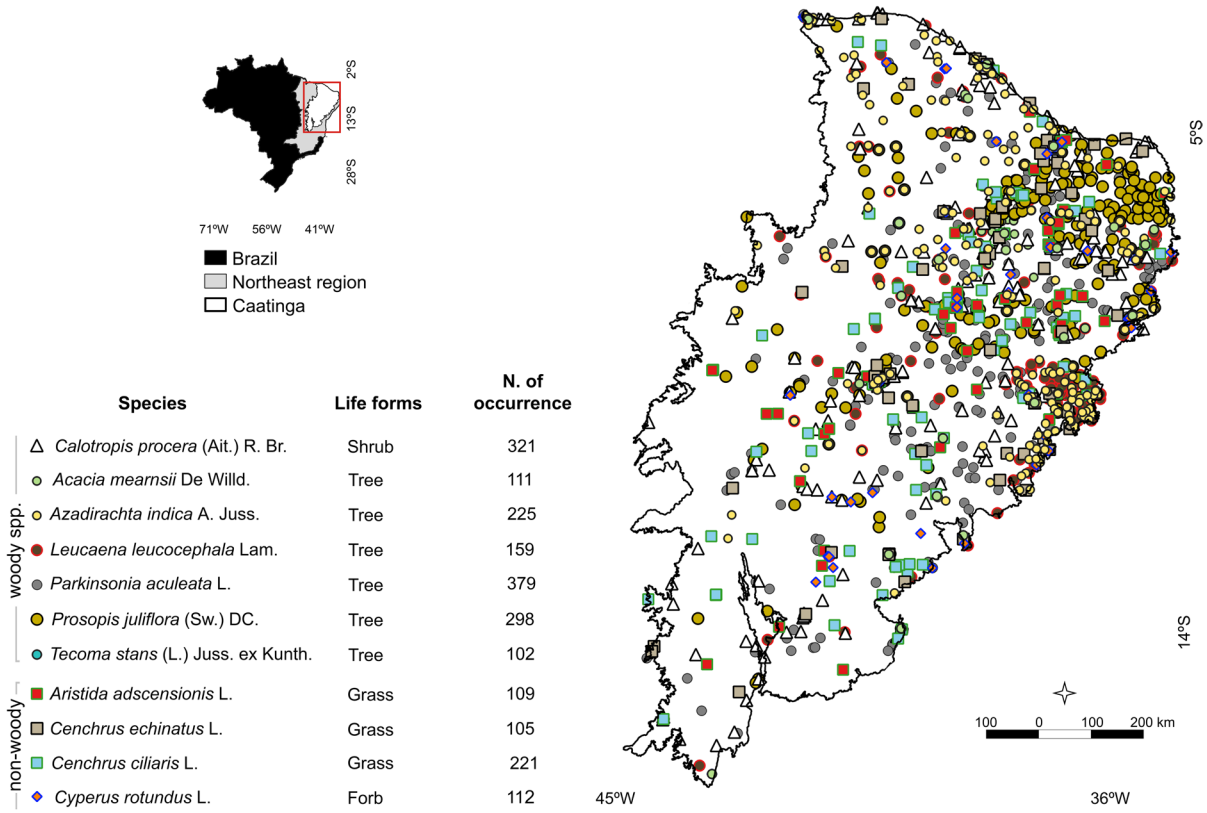


Fig. 1 Species (n = 11) that were modeled based on the number of georeferenced points available for the Caatinga. Only species with a minimum of 100 points and area under the curve (AUC) values above 0.7 were included

zones potentially represent regions where combinations of functionally distinct invasive species may persist or expand under changing climatic conditions. Although some co-occurrence is already observed in the present, available occurrence records suggest that these combinations are relatively recent, likely emerging over the past decades due to ongoing invasion processes. This interpretation is based on the temporal metadata associated with species occurrence records, primarily from GBIF and SpeciesLink, which indicate that most records within co-occurrence zones were collected between 2008 and 2023. Although the age of individual plants at the time of sampling is unknown, this pattern suggests that the establishment of these combinations is relatively recent.

The spatial extent of these zones was compared across time periods and scenarios (optimistic and pessimistic) to quantify their persistence, contraction, or expansion. While based on visual inspection and not on modeled biotic interactions, this approach provides a spatially grounded perspective on how climate change may influence the structure and continuity of invasion patterns involving distinct functional groups.

Results

The modeling accuracy for the 11 species included (i.e., μ-AUC > 0.7) was satisfactory for both climate change scenarios within their respective time interval (Table 2).

The annual mean temperature (Bio1) and annual precipitation (Bio12) were the environmental variables that most affected the majority of the modeled species in the scenarios assessed at each time interval, followed by monthly total precipitation (pr), isothermality (Bio3), seasonal precipitation (Bio15), precipitation of the driest quarter (Bio17), and precipitation of the coldest quarter (Bio19). The

Table 2 Mean AUCs (Area Under the Curve) for the 11 modeled invasive plant species in the Caatinga, in each climate change scenario over time

Interval	AUC Optimistic scenario	AUC Pessimistic scenario
2021 a 2040	0.721	0.755
2041 a 2060	0.765	0.756
2061 a 2080	0.763	0.762
2081 a 2100	0.703	0.726

latter variable was considerably less important in predicting the potential distribution of the modeled species in the Caatinga (Fig. 2).

Consensual distribution in the Caatinga

The suitability for biological invasion by the 11 modeled species remained consistent across different scenarios and time periods, with the only notable change being in the extent of areas potentially susceptible to invasion (measured in km^2). Regions highly suitable for biological invasions are primarily located in the north and east of the study area, spanning from coordinates −4.2305°, −39.5503° to −6.5909°, −35.7894° (Fig. 3).

Once low-suitability areas were excluded from the calculation (a conservative approach), the Caatinga is left with a total potential area of 195,982 km^2 (23.5% of its total area) that is suitable for biological invasions in the optimistic scenario, and of 226,003 km^2

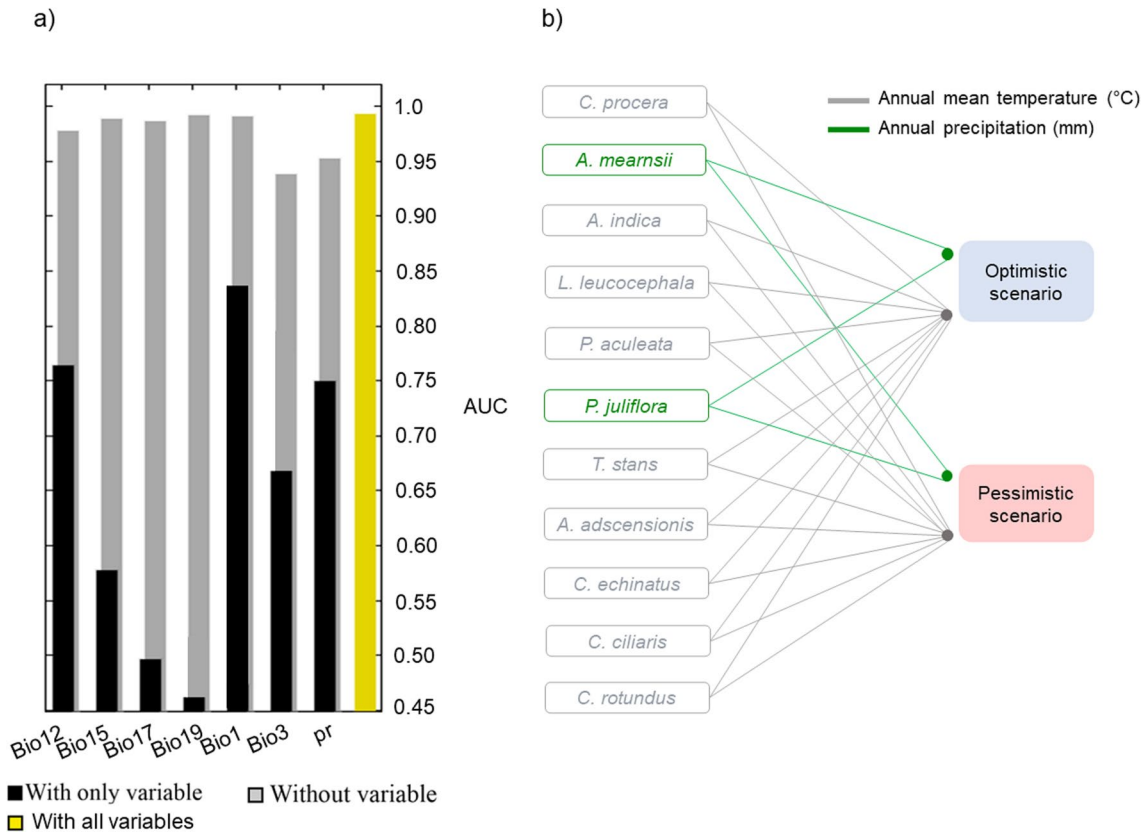


Fig. 2 **a** Importance of the environmental variables in projecting the distribution of 11 invasive species (Jackknife test) in the Caatinga ecosystem, Brazil. The bars indicate the training gain: using only each individual variable (black bars), using all variables together (yellow bar), and the reduction in gain when each variable is omitted from the complete model (gray bars); **b** Main variables explaining the distribution of each invasive species under optimistic and pessimistic scenarios. Species labeled in gray are mainly influenced by annual mean temperature, while species in green are primarily affected by annual precipitation. Lines link each species to the dominant variable shaping its future distribution

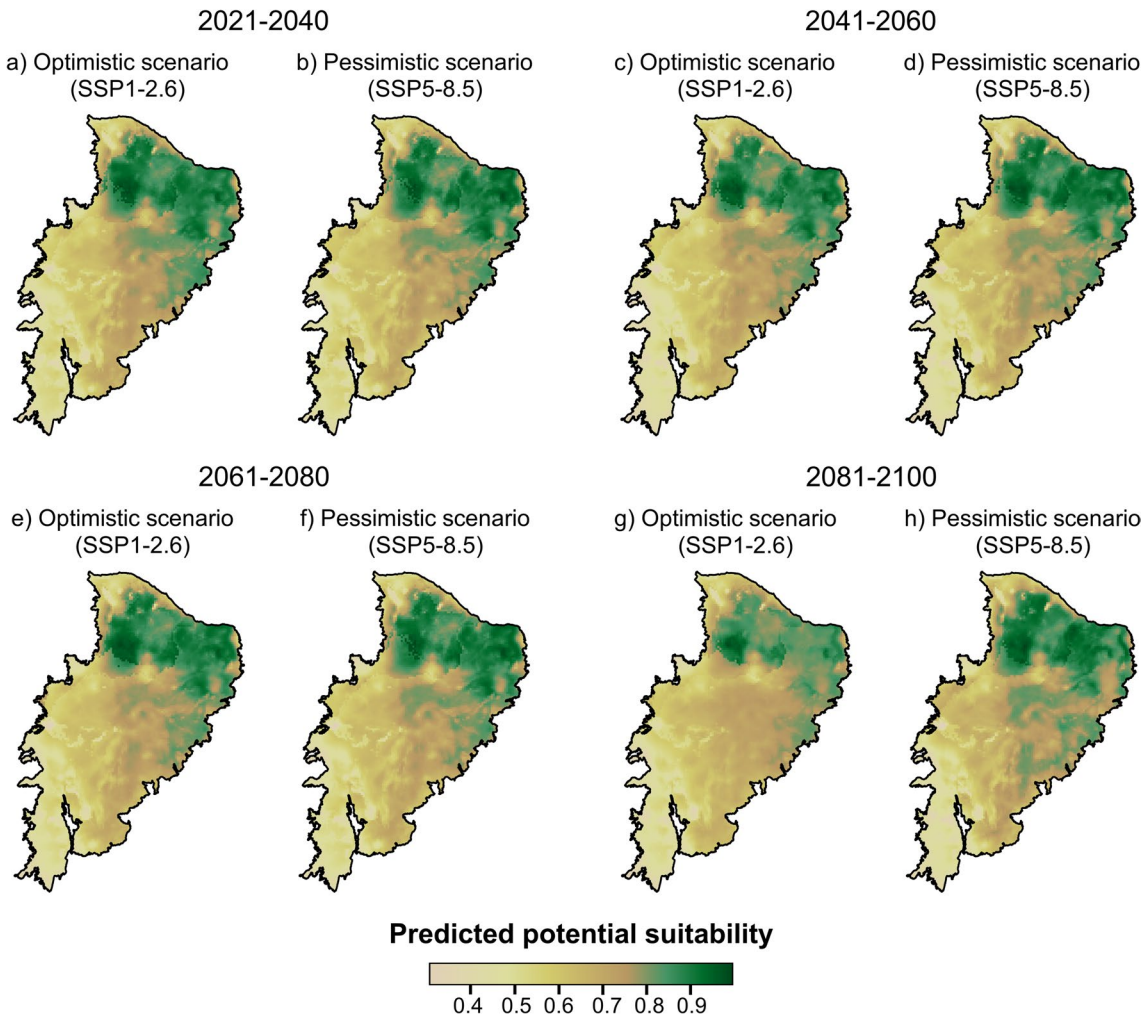


Fig. 3 Projected habitat suitability for 11 invasive plant species in the Caatinga ecosystem, Brazil, across four future time periods (2021–2040, 2041–2060, 2061–2080, and 2081–2100) under two climate scenarios: optimistic (SSP1-2.6) and pessimistic (SSP5-8.5). Panels a–h show predicted potential suitability, where the color gradient represents habitat suitability scores from low (beige) to high (green). Areas with medium suitability have scores between 0.8 and 0.89, while areas with high suitability have scores above 0.9

(27%) in the pessimistic scenario for the 2021–2040-time interval (Table 3). Following this period, in the optimistic scenario, the area suitable for invasion is projected to decrease, reaching 124,494 km^2 in the final interval. Similarly, in the pessimistic scenario, the suitable area is also projected to decrease, reaching 162,202 km^2 (Table 3).

Functional group distribution

The projected impact of climate change suggests that, in the initial period (2021–2040), high-suitability areas (suitability > 0.9) are expected to cover between approximately 30,000 and 58,000 km^2 across the functional groups (Fig. 4a). During this period, non-woody species are projected to occupy the largest high-suitability areas, a trend that persists across subsequent decades under both climate scenarios (Fig. 4). Woody species exhibit a modest expansion in the early period but show a consistent decline in high-suitability areas (> 0.9) over time, under both the optimistic and pessimistic scenarios. The medium-suitability category (0.8–0.89) was excluded to avoid visual clutter and highlight areas with the

Table 3 Suitable areas (km^2) for biological invasion under climate change scenarios over the years

	2021–2040		2041–2060		2061–2080		2081–2100	
	Opt	Pe	Opt	Pe	Opt	Pe	Opt	Pe
High	44,664	56,210	60,234	33,556	54,468	30,302	19,917	41,002
Medium	151,318	169,793	147,814	187,500	180,211	191,120	104,577	121,200
Total	195,982	226,003	208,048	221,056	234,679	221,422	124,494	162,202

High = High suitability for biological invasion; Medium = Medium suitability; Opt = Optimistic scenario and Pe = Pessimistic scenario

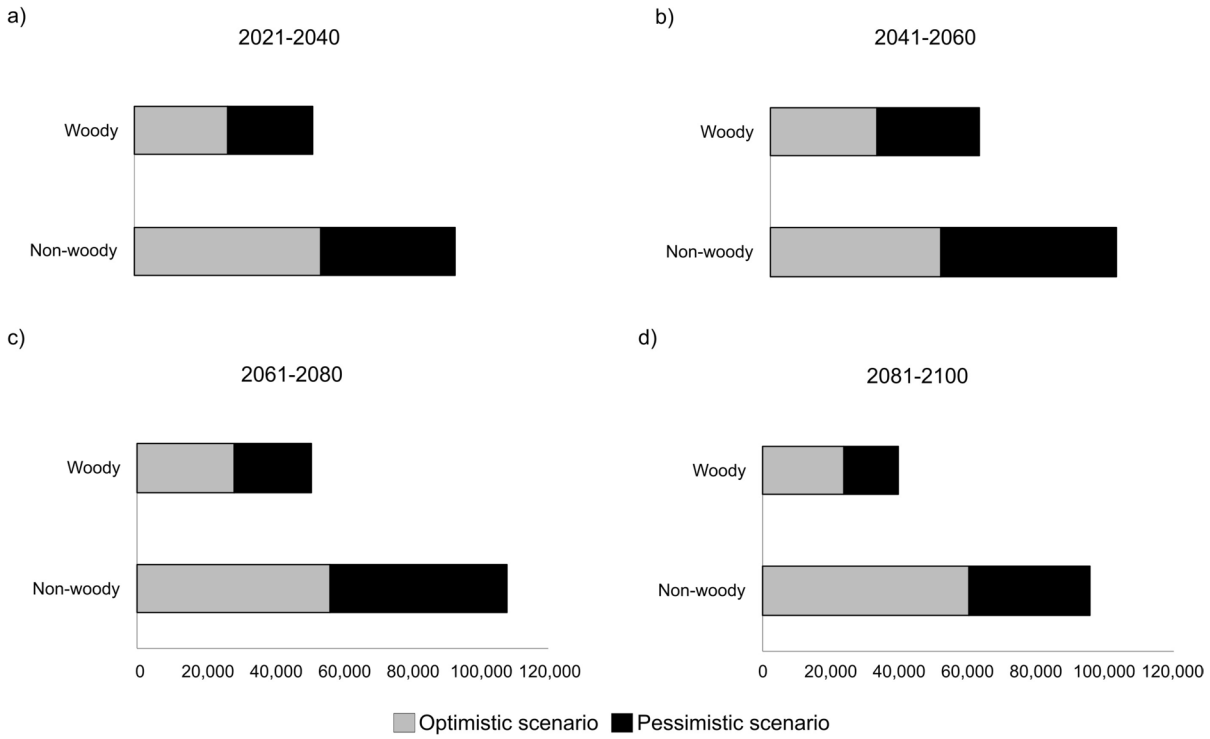


Fig. 4 Projected high-suitability areas for potential invasion by two functional groups of invasive species (woody and non-woody) in the Caatinga ecosystem (Brazil), across four future time periods: **a** 2021–2040, **b** 2041–2060, **c** 2061–2080, and **d** 2081–2100. Bars represent areas (km^2) under optimistic (gray) and pessimistic (black) climate scenarios

highest likelihood of supporting invasions, allowing for a more conservative and ecologically meaningful interpretation.

Species with broader invasion range

In high suitability areas of both scenarios, invasive species such as the grasses *Cenchrus ciliaris* L. and *Cenchrus echinatus* L., the tree *Prosopis juliflora* (Sw.) DC., and the shrub *Calotropis procera* (Ait.) R. Br. stand out, especially in the optimistic scenario, with projected occupied areas of 34,959 km^2, 19,937 km^2, 5,629 km^2, and 6,000 km^2, respectively (Fig. 5).

Persistence and consolidation of functional co-occurrence zones

By the end of the century, a 55% reduction in high-suitability area is projected under the optimistic scenario, corresponding to a loss of approximately 17,706 km^2 (Fig. 6b), along with a 50% decrease

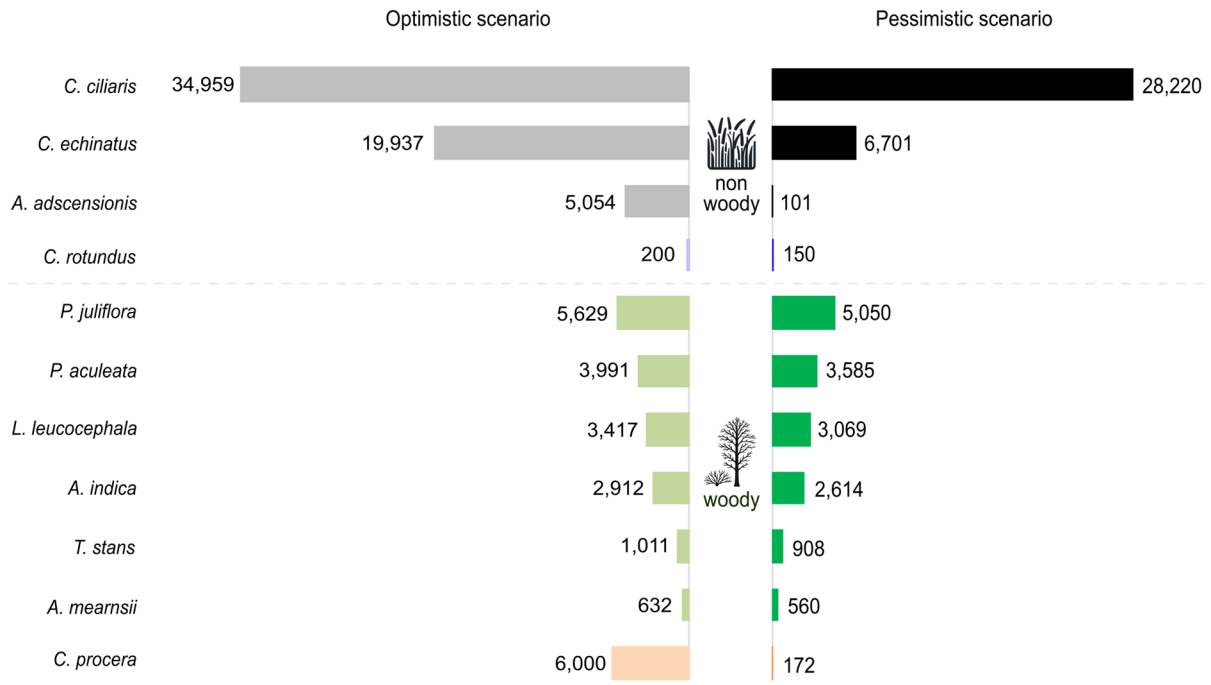


Fig. 5 Projected high-suitability areas (km^2) for 11 invasive plant species in the Caatinga ecosystem (Brazil) by the end of the twenty-first century (2081–2100), under optimistic (left bars) and pessimistic (right bars) climate scenarios. Species are grouped by functional type: non-woody (top) and woody (bottom), as indicated by the respective icons

in the number of invasive occurrences, considering both functional groups. Similarly, under the pessimistic scenario, a 28% reduction in suitable area is projected, equivalent to about 5,002 km^2, accompanied by a 66% decrease in occurrences (Fig. 6d).

One specific region (–6.304°, –38.220°), however, remained suitable and continued to support overlapping occurrences from both woody and non-woody species across both periods. In this area, co-occurrence extent declined by about 202 km^2 (4.58%) under the optimistic scenario and 2,937 km^2 (55%) under the pessimistic one. Although both scenarios indicate habitat contraction, the projected persistence of overlapping suitability in this region may reflect a localized retention or consolidation of relatively recent co-occurrence patterns, shaped by previous invasion dynamics. This stability, despite broader losses elsewhere, could represent a site of ecological relevance where functionally distinct invaders have already converged and may continue to interact under future climatic conditions (Fig. 6b–d).

Discussion

This study used climatic and georeferenced data to assess how climate change may influence the distribution of invasive plant species in the Caatinga, the world's largest seasonally dry tropical forest (SDTF). By modeling the potential distribution of 11 target species, we identified areas with high environmental suitability for biological invasions and examined how these patterns may shift under future climate scenarios. While invasive species were initially expected to expand their geographic range due to climate change, our findings indicate that this expansion may be more limited than anticipated. In the next few decades, non-woody and woody species may have new opportunities for invasion in areas that will maintain a relatively milder climate, with average annual temperatures ranging from 24 to 27 °C and higher annual precipitation (900–1000 mm) (INMET 2020). However, the overall trend reveals that non-woody species are projected to occupy the largest high-suitability areas throughout the century, while woody

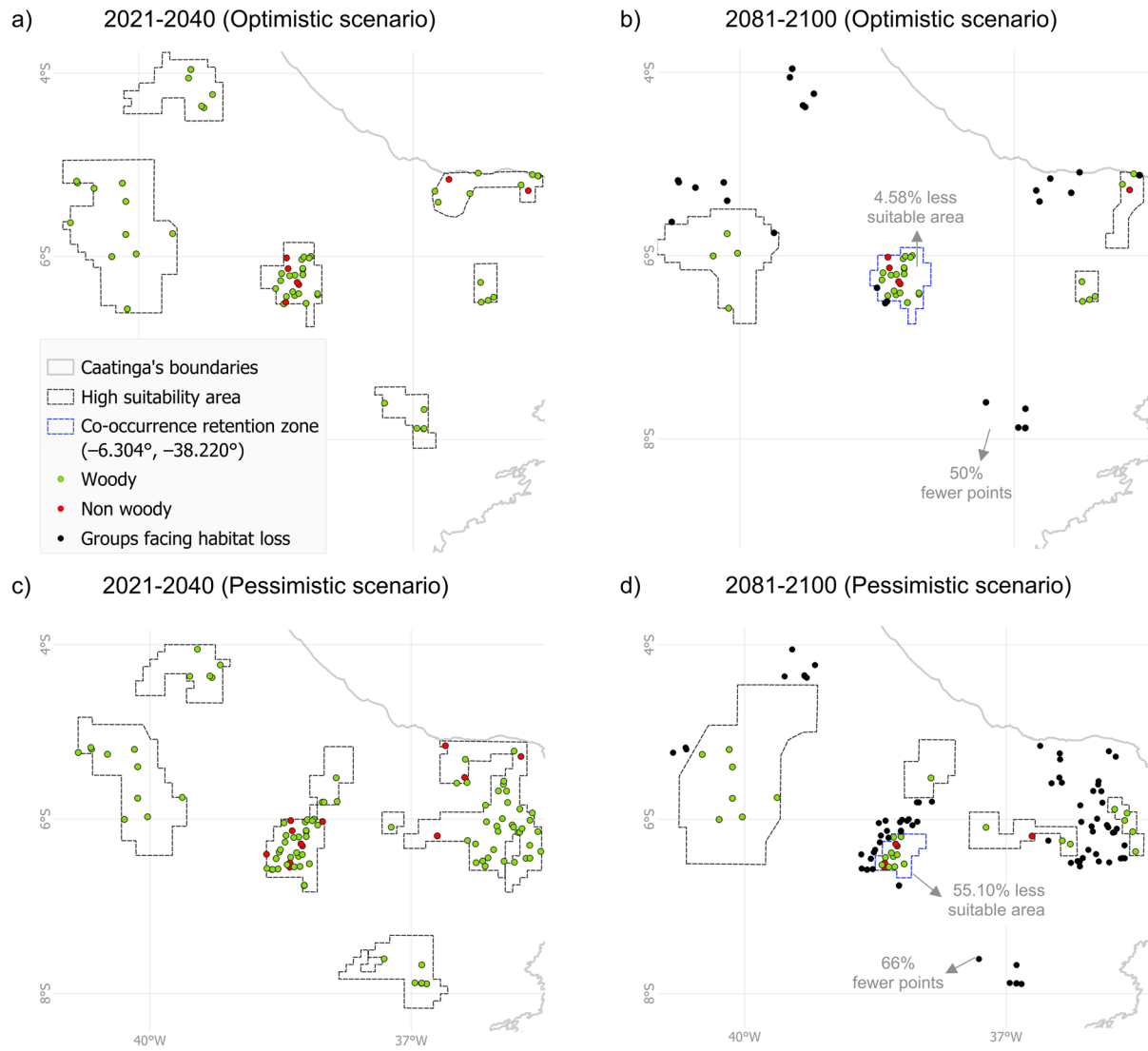


Fig. 6 Changes in high-suitability areas (dashed black lines) where functional co-occurrence between woody and non-woody invasive species already occurs and is projected to persist or decline in the Caatinga ecosystem (Brazil) comparing early (2021–2040) and late century (2081–2100) under optimistic **a**–**b** and pessimistic **c**–**d** scenarios. A retention zone (blue outline) highlights a region of sustained overlap, potentially reinforcing co-occurrence patterns already underway. Black points indicate local habitat loss for at least one group

species tend to decline after an initial modest expansion, under both optimistic and pessimistic climate scenarios. Additionally, our projections suggest the retention of functional co-occurrence zones, where multiple invasive species from distinct functional groups are expected to remain overlapping in environmentally suitable areas under future conditions. Although these patterns are theoretical and contingent on species-specific dynamics not fully captured by our models, they may reflect or amplify ecological configurations that have emerged only recently and received limited attention in the Caatinga. As such, they highlight regions where invasion dynamics could be shifting toward assemblages with no clear historical equivalents.

Temperature and precipitation play a pivotal role in plant distribution, reproduction, and adaptation (Criddle et al. 1994; Ringelberg et al. 2023;

Yao et al. 2024), and have proven crucial in defining the suitability of habitats to invasive plants. The decreasing suitability observed here after 2040 is likely due to the anticipated increase in temperature and decline in precipitation in the Caatinga over the coming decades (Koch et al. 2021; Marengo et al. 2020). Research into plant distribution in both semi-arid and temperate climates has underscored the significance of these variables. Much like our findings, these studies have revealed that harsher warming scenarios negatively impact potential areas for invasion (Andersen et al. 2015; Xu Yue et al. 2016).

The areas that are most suitable for invasive plants are primarily located on the north and east of the Caatinga ecosystem, which is due to various factors. One of these factors involves the interplay between temperature and precipitation. As we move away from the coastal regions towards the interior, a pattern emerges where the average temperature rises, while precipitation decreases (Santos et al. 2014). As a consequence, it is plausible that the number of suitable areas for the development of certain species, even if they are highly resilient, may decrease. In contrast, in regions near the coast, when the warm air over the land comes into contact with the cooler ocean waters, the maritime effect occurs, resulting in cloud formation and possibly precipitation, which may promote plant invasions in these regions (Dantas 2016; Santos et al. 2014).

In terms of functional groups, woody species are projected to occupy smaller high-suitability areas over time, particularly toward the end of the twenty-first century. Interestingly, the georeferenced occurrence points of certain woody species are concentrated in regions marked by geographical barriers, such as the Serra da Borborema (eastern Caatinga) and the Rio São Francisco (southern Caatinga). These features can limit dispersal and restrict the expansion of invasive populations (Alexander et al. 2022). However, some species may still gradually colonize adjacent slopes and mountaintops over time, aided by wind or animal-mediated dispersal mechanisms (He et al. 2023; Iseli et al. 2023; Richardson et al. 2000). While certain individuals may overcome these physical barriers, understanding how climate change may influence local climatic conditions by altering temperature and precipitation patterns remains essential to predict future invasion routes and species spread (Moura et al. 2023; Prochazka et al. 2024). This topic deserves further exploration in future studies.

Projections for non-woody species suggest that this group may occupy larger high-suitability areas by 2100, even if the expansion is not substantial over time. This pattern is likely driven by the dominance of invasive grasses within this group, which tend to exhibit high water use efficiency, strong acclimatization capacity, rapid propagule dispersal, and elevated seed production within a single season. Additionally, grasses often benefit from a broad array of dispersal agents, including wind, water, and animals, as exemplified by species such as *C. ciliaris* (Almeida et al. 2015; Ghirardo et al. 2022; Pertierra et al. 2023). These functional traits may allow them to exploit dynamic or disturbed environments more effectively, maintaining their suitability across a range of future climatic conditions in the Caatinga.

Although the number of records for the studied species has increased over the past 12 years (2011–2023) (Fabricante et al. 2021), their spread in the Caatinga remains constrained by environmental thresholds such as water availability and temperature extremes. Nonetheless, these invaders often exhibit broader ecological tolerances than native flora, particularly under disturbance regimes. Even if climate change reduces overall invasion potential in some areas, the localized persistence of functionally distinct species may still drive ecological restructuring (Funk 2013; Heberling and Fridley 2013; O'Loughlin et al. 2021). We identified a single region where woody and non-woody invaders are both projected to persist under high environmental suitability, which may represent a zone of functional co-occurrence retention in the Caatinga. While this study does not simulate biotic interactions or full community structure, the projected overlap suggests that the region may already be staging new ecological interactions among invasive species. Historical records show that invasive plants can alter community composition over relatively short timeframes, as seen in post-colonial introductions across tropical regions (Pyšek et al. 2020). Despite the limited temporal scope of our 80-year projections, this overlap may signal an incipient form of ecological reorganization. Even if localized or restricted, such patterns could have cascading effects on biodiversity, ecosystem functioning, and trophic stability in the Caatinga (Monteiro et al. 2023; Pyšek et al. 2020; Rai and Singh 2020).

Beyond spatial patterns, grasses like *C. ciliaris* exemplify how these species can disrupt trophic structures. Its rapid growth reduces shelter for native fauna and elevates wildfire risks, partly due to its extensive and dense root systems (Boone et al. 1998). Climate change disruptions might provide opportunities for such species, especially if they are not dependent on specific ecological relationships (Rhodes et al. 2021). Another case is *P. juliflora*, a species that has successfully established in the Caatinga, aided by efficient seed dispersal mechanisms involving livestock (David et al. 2017; Nascimento et al. 2020). This ecological flexibility contrasts with many native specialist plants, which rely on a narrower range of seed dispersers and pollinators and are therefore more susceptible to the adverse effects of environmental change (Duffy and Johnson 2017; Gambel and Holway 2023; Landim et al. 2025). As such, even as climate change influences habitats for invasive species, they might maintain an edge over specialized native counterparts (Bellard et al. 2018).

Effective management of the Caatinga requires a strategic and multifaceted approach. By identifying the northern and eastern regions as particularly vulnerable to plant invasions, our results highlight priority areas for targeted conservation and intervention strategies. These regions demand dedicated studies and tailored management plans that consider both current and projected climate scenarios. Rigorous monitoring, combined with tools such as species distribution modeling, georeferenced data, and remote sensing, is essential to anticipate and prevent the spread of invasive species (Tuanmu and Jetz 2015). Efforts to restore degraded areas and prioritize native biodiversity in land-use planning are critical for maintaining ecosystem resilience in the Caatinga (Messier et al. 2022). In addition, public awareness and community involvement are key to supporting successful management outcomes (Dechoum et al. 2019). Campaigns that discourage the use of invasive species and promote conservation practices can help safeguard the Caatinga's biodiversity and reinforce its value as a unique and irreplaceable natural heritage (Antongiovanni et al. 2022; Eylering et al. 2025).

Conclusion

The Caatinga, the world's largest seasonally dry tropical forest (SDTF), faces complex challenges from invasive plant species, especially under the pressures of climate change. Our findings show that a variety of invasive species, particularly non-woody plants such as grasses, are more likely to persist and expand under future climatic conditions. These species exhibit functional traits such as rapid reproduction and high dispersal capacity, which may allow them to thrive even as the environment becomes hotter and drier. In contrast, woody species are projected to experience a decline in suitable areas, especially toward the end of the century. Due to the Caatinga's vast extent and environmental heterogeneity, specific regions, especially in the northern and eastern portions, appear more susceptible to invasion and should be prioritized for monitoring and management efforts. Importantly, we identified one region where woody and non-woody invasive species are projected to continue co-occurring under favorable environmental conditions. This spatial overlap suggests that co-occurrence patterns, involving functionally distinct species not historically found together in the Caatinga, not only already exist but may persist or even expand in the future. While this does not imply the formation of entirely new communities, it highlights subtle shifts in invasion dynamics that may lead to novel species associations over time, warranting further investigation. Crucially, the relatively limited future expansion of many invasive species does not imply reduced ecological risk. On the contrary, it may reflect that invasives are already established in vulnerable regions, where their persistence could amplify the ecological impacts of climate change on native biodiversity, which tends to be more sensitive (Gambel and Holway 2023). Proactive measures such as forest restoration, increased native species diversity, and the incorporation of biodiversity into land-use planning are essential to strengthen the resilience of the Caatinga. As with many global ecosystems, the future of the Caatinga depends on forward-looking strategies that reconcile conservation goals with the realities of a changing climate.

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Author contributions CLCS did the modeling and statistical analyses. All authors contributed to the conception and design of the study, participated in writing and/or critically evaluated the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

Appendix 1: Description of bioclimatic variables used in the models

Variable	Description
Bio1 (°C)	Annual Mean Temperature
Bio2 (°C)	Mean Diurnal Range (Mean of monthly (max temp—min temp))
Bio3	Isothermality (Bio2/Bio7 × 100)
Bio4	Temperature Seasonality (standard deviation × 100)
Bio5 (°C)	Max Temperature of Warmest Month
Bio6 (°C)	Min Temperature of Coldest Month
Bio7	Temperature Annual Range (Bio5—Bio6)
Bio8 (°C)	Mean Temperature of Wettest Quarter
Bio9 (°C)	Mean Temperature of Driest Quarter
Bio10 (°C)	Mean Temperature of Warmest Quarter
Bio11 (°C)	Mean Temperature of Coldest Quarter
Bio12 (mm)	Annual Precipitation
Bio13 (mm)	Precipitation of Wettest Month
Bio14 (mm)	Precipitation of Driest Month
Bio15 (mm)	Precipitation Seasonality (Coefficient of Variation)
Bio16 (mm)	Precipitation of Wettest Quarter
Bio17 (mm)	Precipitation of Driest Quarter
Bio18 (mm)	Precipitation of Warmest Quarter
Bio19 (mm)	Precipitation of Coldest Quarter
Tn (°C)	Monthly minimum mean temperature
Tc (°C)	Monthly maximum mean temperature
Pr (mm)	Monthly total precipitation

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