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ORIGINAL RESEARCH

Distribution of the baraúna tree is threatened by climate change, land-cover change, and biological invasions in the Brazilian Caatinga

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Abstract
Multiple drivers shape biodiversity loss worldwide. Land-use change and biological invasions are major direct pressures on species, while climate change increasingly alters species distributions and community dynamics, often intensifying other stressors. However, these factors are still insufficiently integrated into Ecological Niche Modeling (ENM) studies. We quantified the potentially suitable area for *Schinopsis brasiliensis* Engl., a tree species of high ecological importance in the Caatinga domain, considering the combined effects of climate change, land-cover change (LCC), and invasion by the exotic species *Neltuma juliflora* (Sw.) Raf. (hereafter, *Neltuma* spp.), known to reduce native plant abundance. We modeled the potential distributions of *S. brasiliensis* and *Neltuma* spp. under current and future scenarios using ENMs. Simulations of LCC were used to quantify anthropization within suitable areas for *S. brasiliensis*, and species models were combined to identify spatial overlap. Currently, *S. brasiliensis* occupies approximately 702,176 km² of suitable area, with projections indicating a reduction to 467,927 km² by 2081–2100. When LCC is incorporated, projected losses exceed 28% in most scenarios. Overlap with *Neltuma* spp. was total across all projections. Our results indicate that *S. brasiliensis* may undergo substantial contractions of climatic suitable areas in the Caatinga by the end of the century due to LCC. In overlapping areas, *Neltuma* spp. may act as an additional pressure, limiting or preventing the persistence of *S. brasiliensis*. This study highlights climatically suitable areas with lower future anthropization risk and underscores the importance of managing *Neltuma* spp. to conserve key native species in the Caatinga.

Keywords Anthropization · Exotic invasive species · Ecological niche modeling · Seasonal tropical dry forest

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Introduction

Multiple anthropogenic drivers contribute to biodiversity loss in terrestrial ecosystems. Among them, land-use and land-cover change act as major direct pressures, while biological invasions also play a substantial role (Díaz et al. 2019). Climate change increasingly alters species distributions and community composition, amplifying the effects of other stressors and intensifying extinction risk (Aitken et al. 2008; Bellard et al. 2012; Urban 2015; Warren et al. 2018). Ecological niche models (ENMs) have been widely used to model species-environment relationships using climatic variables and to evaluate model transferability across climatic gradients, forming the basis for their application in climate change projections (Guisan and Thuller 2005; Hijmans and Graham 2006). However, because they are often limited to climatic variables, conventional correlative modeling approaches frequently overlook other important factors that may also strongly influence species distributions (Frans and Liu 2024). To make potential distribution projections more realistic and robust, it is essential to incorporate additional abiotic stressors and biotic interactions, such as land-cover change (LCC) and biological invasions (Guisan and Thuller 2005; Araújo and Luoto 2007; Urban et al. 2016; Tourinho et al. 2022).

The Seasonal Dry Forest region of the Caatinga is considered one of the most susceptible Brazilian ecosystems to these drivers of biodiversity change (Torres et al. 2017; Araujo et al. 2023). Climatic projections forecast an increase in temperature and a decrease in precipitation in the region, resulting in longer and more intense drought periods (Torres et al. 2017; Silva et al. 2023). This scenario may lead to both functional and taxonomic losses in biological communities across its territory (Moura et al. 2023). Furthermore, in just the last 40 years, approximately 26.36% of its primary vegetation has been lost due to land-cover change, mainly driven by the expansion of human activities such as agriculture (Projeto MapBiomas 2021). In the Caatinga, this process is recognized as the main driver of vegetation change (Araujo et al. 2023). The intense disturbance of natural areas caused by anthropogenic activities also promotes the spread of numerous exotic invasive species, which drive biological invasion processes in the Caatinga (Almeida et al. 2015; Pinto et al. 2020; Dechoum et al. 2024). Together, land-cover change and biological invasions may intensify the exclusion of native species due to their synergistic effects (Didham et al. 2007; Gutiérrez-Cánovas et al. 2020).

Among the Caatinga species vulnerable to these impacts is *Schinopsis brasiliensis* Engl., commonly known as "baraúna," a tree from the Anacardiaceae family with high ecological, medicinal, and economic value (Carvalho 2008; Kiill and Lima 2011; Barreto et al. 2022). Despite its importance, *S. brasiliensis* has been threatened by multiple factors, including overexploitation (Martinelli and Moraes 2013) and the conversion of natural Caatinga habitats for various purposes, such as pasture, agriculture, and urban infrastructure (Kiill and Lima 2011; Ramos et al. 2023). Additionally, studies have reported population declines of *S. brasiliensis* due to the invasion of *Neltuma juliflora* (Sw.) Raf. (formerly *Prosopis juliflora* (Sw.) DC.) (Pegado et al. 2006; Andrade et al. 2009, 2010). This is a tree species belonging to the family Fabaceae, native to South, Central, and North America, and typically occurring in semi-arid environments (Pasha and Reddy 2024). Introduced into the Caatinga in the 1940s for use as forage, charcoal, firewood, and fence posts (Pegado et al. 2006), this species currently invades almost the entire Brazilian Northeast, with the exception of the state of Maranhão (Flora e Funga do Brasil 2026). This species competes with native plants

in Caatinga, hindering their development and increasing mortality rates (Fabricante and Siqueira-Filho 2013; Souza Nascimento et al. 2014).

Given the challenges posed by climate change, LCC, and biological invasions, the adoption of integrative approaches is necessary to assess the combined effects of these factors on species distributions. Accordingly, in this study we applied an integrative framework to evaluate how these stressors may affect the potential distribution of *S. brasiliensis* in the Caatinga. Specifically, we aimed to (i) model the climatic suitability of *S. brasiliensis* under current and future scenarios using ENMs, (ii) quantify the overlap between climatically suitable areas for *S. brasiliensis* and the invasive species *N. juliflora*, and (iii) assess the proportion of this overlapping area potentially influenced by anthropized environments as a result of LCC. We expect that the climatically suitable areas for *S. brasiliensis*, as estimated by the ENMs, will be reduced both by overlap with *N. juliflora* and by the presence of anthropized areas. Moreover, we expect that this integrative approach increases the robustness and reliability of assessments of the potential distribution of *S. brasiliensis* (Medeiros et al. 2023).

Methods

Study area

The study was carried out in the Caatinga, a seasonally dry forest with a total area of approximately 862×10^3 km² that is largely located in Northeast Brazil (IBGE 2019). The predominant climate is Bsh hot semi-arid, according to Köppen's classification (Alvares et al. 2013). The region has high temperatures, with annual averages between 25° and 30 °C and little variation (Sampaio 2003). On the other hand, precipitation can present great temporal and spatial variation, generally ranging between 400 and 1200 mm annually, but reaching 1800 mm on plateaus (Tabarelli et al. 2017). Currently, a large part of the native forest territory of the Caatinga is extremely anthropized, mainly due to chronic disturbances, which arise from the cumulative effect of multiple human impacts that promote slight but continuous changes in the composition, structure, and functioning of ecosystems (Antongiovanni et al. 2019) (e.g. livestock grazing, timber extraction, and burning).

Ecological niche modeling (ENM)

Species occurrence data

We grouped the occurrence records of *N. juliflora* with those of *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth, a species that also currently invades the Caatinga (Pinto et al. 2020) and co-occurs with *N. juliflora*. This grouping was adopted because these species share similar morphological and ecological characteristics, which may have led to misidentifications in herbarium records (Fabricante and Siqueira-Filho 2013; Oliveira et al. 2017a). This approach allowed us to avoid the loss of climatic information for *N. juliflora* that could result from excluding records mistakenly identified as *P. pallida*. In addition, this grouping is unlikely to introduce undesirable noise into the ecological niche models (ENM), since the climatic niches of the two species are highly similar (Oliveira et al. 2017a). Therefore,

hereafter this species grouping is referred to as *Neltuma* spp. (see Pasiecznik et al. 2001; Mengistu et al. 2023).

The occurrence records used in the ENM were obtained from the entire range of occurrence of the species evaluated in the online databases Global Biodiversity Information Facility (*S. brasiliensis*: https://doi.org/10.15468/dl.bhb26j, *Neltuma* spp.: https://doi.org/10.15468/dl.w7zqxw) and SpeciesLink (https://specieslink.net/). The use of records from both native and introduced ranges is widely adopted in ENM studies of invasive species. This approach allows the inclusion of the full climatic niche of *Neltuma* spp., resulting in more robust models (Shabani and Kumar 2015).

To eliminate noise and uncertainties in the models (Varela et al. 2014), the occurrences of the studied species were subjected to a cleaning process before being used. For this purpose, we used the CoordinateCleaner package (Zizka et al. 2019) in the R software to exclude duplicate coordinates and records with collection errors. Additionally, records before 1990 were excluded to prioritize those with higher precision. To reduce spatial autocorrelation (Boria et al. 2014; Boucher-Lalonde and Currie 2016), a thinning was performed, excluding points within 5 km of others, thus preventing more than one occurrence of the species from being in the same cell of the climate variable (Jarnevich et al. 2015). After this stage, 468 records were retained for *S. brasiliensis* and 964 for *Neltuma* spp (Fig. 1).

Calibration area (M) delimitation

The calibration areas for *S. brasiliensis* and *Neltuma* spp. were defined as the terrestrial ecoregions (Dinerstein et al. 2017; Fig. 1) with at least one confirmed occurrence record of each species. For *Neltuma* spp., this area encompassed ecoregions from both its native and invaded ranges. For *S. brasiliensis*, portions of certain ecoregions were excluded due to the absence of occurrence records or supporting evidence of its presence. This cut was made using a convex polygon connecting the points of occurrence (adapted from IUCN, 2024). Then, a buffer of ~1° (~100 km) was applied to this polygon, and the resulting area was used as a clipping mask for the ecoregions (see Simões et al. 2020). In both delineations, the Caatinga region was already included within the selected ecoregions, as occurrence records for both species were available in this biome (Fig. 1).

Climatic variables selection

A set of 19 climate variables from the present and future was obtained from WorldClim 2.0 at a resolution of 2.5 min (~4.5 km² at the equator) (Fick and Hijmans 2017). To exclude variables with high collinearity, a Spearman correlation analysis was performed, and those with values lower than 0.7 were retained (Dormann et al. 2013; Table 1).

For future projections, two periods (2041–2060 and 2081–2100) were evaluated, based on two Shared Socioeconomic Pathways (SSPs), SSP1-2.6, which assumes a reduction in greenhouse gas emissions and low radiative forcing (i.e., variation in the balance of solar radiation entering and leaving the Earth), and SSP5-8.5, which assumes a high concentration of these gases (O'Neill et al. 2016). These SSPs were selected because they represent plausible extremes of future climate trajectories, including an optimistic scenario (SSP1-2.6) and a pessimistic scenario (SSP5-8.5). In addition, these scenarios are also among the most frequently used SSPs in ENM studies, facilitating comparisons with previous work.

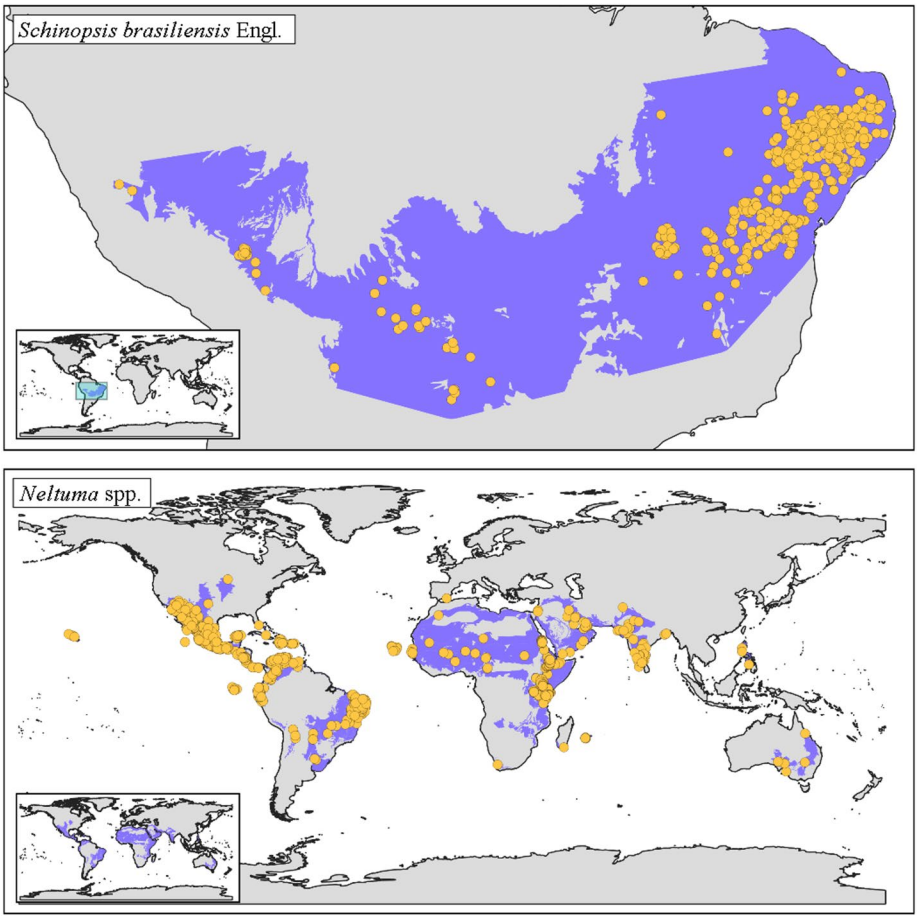

Fig. 1 Geographic occurrence records and calibration areas (M) for *Schinopsis brasiliensis* Engl. and *Neltuma* spp. Yellow circles represent the occurrence points used for niche modeling after spatial thinning and cleaning. Purple polygons define the calibration areas (M) used for model training, representing the accessible geographic space for each taxon over relevant evolutionary time scales. Top panel shows the regional distribution of *S. brasiliensis* within South American seasonally dry tropical forests (SDTFs); bottom panel shows the global distribution of the *Neltuma* species complex, reflecting its broader environmental occupancy. Insets indicate the relative position of the study areas on a global scale

The Global Climate Models (GCMs) used were HadGEM3-GC31-LL, EC-Earth3-Veg, and FIO-ESM-2-0 from the Coupled Model Intercomparison Project Phase Six (CMIP6). These GCMs were selected because they show good climate simulation performance in South America (Fan et al. 2020) and particularly in northeastern Brazil (Dantas et al. 2022). To reduce uncertainties in future projections (Fan et al. 2020), projections obtained from each GCM were combined to generate the final models by calculating the mean of suitability projections across GCMs for each period and its respective climate scenario.

Table 1 Set of WorldClim 2.0 variables used to model the distribution of *Schinopsis brasiliensis* Engl. and *Neltuma* spp

Variables	S. brasiliensis	Neltuma spp.
Annual mean temperature	**X**	—
Mean diurnal range	**X**	**X**
Isothermality	**X**	**X**
Min temperature of coldest month	—	**X**
Annual precipitation	**X**	—
Precipitation of wettest month	—	**X**
Precipitation of driest month	—	**X**
Precipitation seasonality	**X**	**X**
Precipitation of driest quarter	**X**	—

Modeling procedure

In this study, we employed an ensemble modeling approach combining multiple algorithms to produce robust and reliable predictions (Hao et al. 2019). The algorithms used were Generalized Additive Models (GAM), Maximum Entropy (MaxEnt), Random Forest (RF), and Generalized Boosted Models (GBM). For *Neltuma* spp., due to its wide distribution, 10,000 pseudo-absence points were used for the models carried out in the GAM algorithm and 10,000 background points in Maxent, while 4,000 were used for *S. brasiliensis* (Barbet-Massin et al. 2012). For the models generated in RF and GBM, an amount of pseudo-absence equivalent to presence was used for both species (Barbet-Massin et al. 2012).

The models generated were validated using the True Skill Statistic (TSS) and Area Under the ROC Curve (AUC) metrics. In the TSS, sensitivity and specificity points are calculated to indicate the models prediction capacity. Thus, values close to or equal to 1 indicate a satisfactory prediction and values lower than or close to 0 indicate low prediction capacity (Allouche et al. 2006). According to Metz (1986), AUC values between 0.8 and 0.9 are considered good, whereas values above this are classified as excellent performance.

The occurrence points for the two species were separated into a proportion of 70% for training and 30% for testing (Zurell et al. 2020). Models were fitted using four algorithms (GAM, GBM, Maxent, and RF), resulting in a total of 20 calibrated models per species (5 runs × 4 algorithms) (Table S1). Models with TSS > 0.5 and AUC > 0.8 were selected and integrated to generate the final ensemble model. The models were generated from the "Biomod2" R package (https://biomodhub.github.io/biomod2/, Figs. S1 and S2). This package was also used to obtain the contribution of the variables for each species. Subsequently, the models for each species were cut based on the limits provided for Caatinga by IBGE (2019) and binarized using the threshold values that maximized the TSS (Guisan et al. 2017; Table S2).

Land-cover change

To estimate the extent of the climatically suitable area resulting from the ecological niche models may become unavailable for the occurrence of *S. brasiliensis* in the future due to land-cover change (LCC), we used projections provided by Zhang et al. (2023). These projections simulate the spatial heterogeneity of land use for different years (2030, 2050, 2070, and 2100) and scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0, SSP4-3.4, and SSP5-8.5), at a resolution of 1 km². We chose to use these projections because of their better performance

compared to the spatial distribution of LCC data used by the Intergovernmental Panel on Climate Change (IPCC) for developing future climate projections (Hurtt et al. 2020), as they offer finer geospatial detail and greater ability to represent land use in the landscape. LCC mapping is spatialized using the following land-use classes: Cropland, Forest, Grassland, Urban, Barren and Water (Zhang et al. 2023).

The LCC projections were resampled to match the resolution of the climate models (~4.5 km² at the equator). After resampling, we grouped and quantified the areas classified as Cropland and Urban to generate a proxy for anthropization resulting from LCC. Since the LCC projections are provided for specific years rather than for time intervals, anthropization for the period 2041–2060 was estimated using the intermediate projection for 2050. For the period 2081–2100, we used the 2100 projection, as no intermediate data are available. The historical layer for 2020, which served as the baseline for the LCC projections (Zhang et al. 2023), was accessed and considered as the present period in this study.

Exotic invasive species

Considering the potential impacts that the invasion of *Neltuma* spp. may have on *S. brasiliensis* (Pegado et al. 2006; Andrade et al. 2009, 2010), we assessed the proportion of suitable areas in which both species could occur in the Caatinga. To do so, the binary climate models of *S. brasiliensis* and *Neltuma* spp. were paired by the same time period and scenario, and the overlapping areas between the two species were quantified. Subsequently, we also calculated the proportion of anthropized environments within the spatially overlapping areas between the species. The combination of the models was performed using the Raster Calculator tool in QGIS software (2025). All cartographic layouts presented in this study were also produced using this software.

Results

All suitability models presented TSS > 0.5 and AUC > 0.8, resulting in a good performance of these metrics in the consensus models for each species (Table 2 and S1). This demonstrates that the models have a good ability to predict the potential distribution of the studied species.

For *S. brasiliensis*, Annual Precipitation was the most important variable (mean = 0.89, SD = 0.01), followed by Isothermality (mean = 0.11, SD = 0.00), while Precipitation Seasonality contributed the least (mean = 0.02, SD = 0.00) (Table 3). For *Neltuma* spp., the variables with the highest contributions were Isothermality (mean = 0.36, SD = 0.00) and Precipitation

Table 2 Model performance for *Schinopsis brasiliensis* Engl. and *Neltuma* spp. based on TSS and AUC metrics

Mean ± SD values are shown for each algorithm, and ensemble results summarize the final combined models

Models	S. brasiliensis		Neltuma spp.	
	TSS	AUC	TSS	AUC
GAM	0.57 ± 0.01	0.85 ± 0.00	0.66 ± 0.03	0.87 ± 0.01
GBM	0.76 ± 0.01	0.90 ± 0.00	0.82 ± 0.01	0.92 ± 0.01
MAXENT	0.68 ± 0.01	0.95 ± 0.00	0.80 ± 0.01	0.96 ± 0.00
RF	0.94 ± 0.01	0.99 ± 0.00	0.82 ± 0.01	0.97 ± 0.00
Ensemble	0.88	0.96	0.94	0.97

Table 3 Mean relative importance (±SD) of climatic variables for *Schinopsis brasiliensis* Engl. and *Neltuma* spp., derived from ensemble models

The most important variables for each species are highlighted in bold

Variables	S. brasiliensis	Neltuma spp.
Annual mean temperature	0.05 ± 0.00	—
Mean diurnal range	—	0.05 ± 0.00
Isothermality	0.11 ± 0.00	**0.36 ± 0.00**
Min temperature of coldest month	—	0.19 ± 0.00
Annual precipitation	**0.89 ± 0.01**	—
Precipitation of wettest month	—	0.25 ± 0.00
Precipitation of driest month	—	0.07 ± 0.00
Precipitation seasonality	0.02 ± 0.00	0.27 ± 0.00
Precipitation of driest quarter	0.05 ± 0.00	—

Table 4 Suitable area for the occurrence of *Schinopsis brasiliensis* Engl. at present and in the future, along with the respective proportions of anthropization due to land-cover change in the Caatinga

Projections	Suitable area (km²)	Change vs. present (km²)	Change vs. present (%)	Anthropized suitable area (km²)	Proportion of anthropized suitable area (%)
Present	702,176	—	—	188,018	26.78
SSP1-2.6					
2041–2060	631,192	-70,984	-10.10	178,776	28.32
2081–2100	606,244	-95,932	-13.70	149,859	24.72
SSP5-8.5					
2041–2060	575,721	-126,455	-18.00	168,793	29.32
2081–2100	467,927	-234,249	-33.40	131,121	28.02

Seasonality (mean = 0.27, SD = 0.00), whereas Mean Diurnal Range had the lowest influence (mean = 0.05, SD = 0.00) (Table 3).

Based solely on climate models, the suitable area for the occurrence of *S. brasiliensis* covered approximately 702,176 km² of the Caatinga biome (Table 4; Fig. 2). In future projections, gradual reductions in suitable areas can be observed across all evaluated periods, with pessimistic scenarios showing the most intense declines, especially between 2081 and 2100, where the suitable area could decrease to 467,927 km² (-33.40%). The present suitable area for *Neltuma* spp. was approximately 862,818 km², encompassing the entire Caatinga territory (Fig. 2, Table S3). The suitable area for *Neltuma* spp. remained unchanged across all future projections evaluated (Fig. 2, Table S4).

When considering anthropization caused by land-cover change (LCC), the reduction in available areas for the occurrence of *S. brasiliensis* in the Caatinga is expected to be further accentuated. Currently, 188,018 km² (26.78%) of climatically suitable areas are already compromised by anthropogenic activities (Table 4; Fig. 2). Most future projections show an increase in the proportion of anthropized areas, despite the reduction in climatically suitable areas (Table 4; Fig. 2). These results indicate that a considerable portion of the climatically suitable area for *S. brasiliensis* may become unsuitable for its occurrence in the future.

Due to the extensive coverage and uniformity of climatically suitable areas for *Neltuma* spp., the overlap with *S. brasiliensis* was complete, regardless of the scenario or period evaluated (Fig. 2, Table S4). Consequently, anthropized environments within the suitable area for *S. brasiliensis* may also be susceptible to invasion of *Neltuma* spp. in the future. Moreover, the remaining conserved and climatically suitable environments for *S. brasilien-*

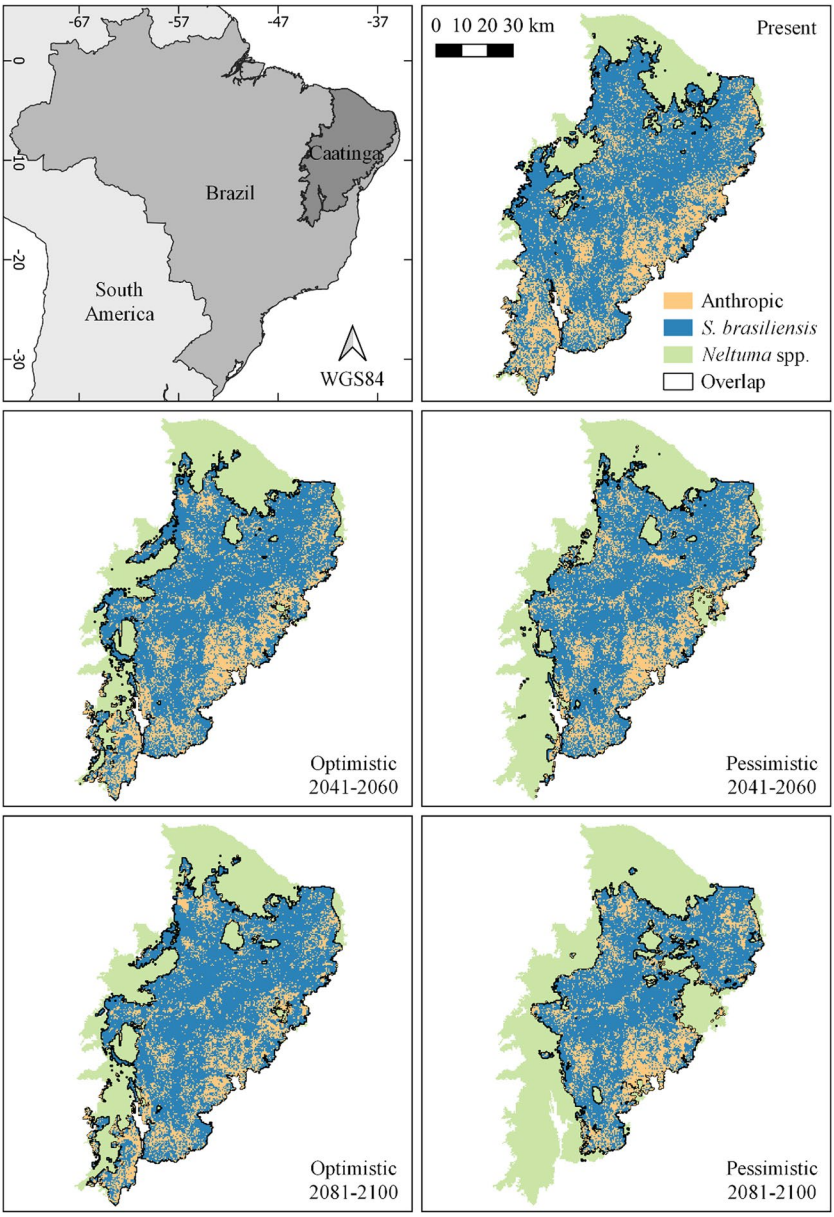

Fig. 2 Spatio-temporal dynamics of climatic suitability and land-cover change for *Schinopsis brasiliensis* Engl. and *Neltuma* spp. in the Caatinga. The maps show the binary projection of ecological niche models for the present and two future time periods (2041–2060 and 2081–2100) under optimistic and pessimistic climate scenarios. Blue areas represent the suitable climatic space for *S. brasiliensis*, while green areas indicate suitability for *Neltuma* spp. The black outline highlights the spatial overlap between both taxa. *Neltuma* spp. was predicted as climatically suitable across the entire Caatinga in all projections. Therefore, the overlap between the two species corresponds entirely to the area predicted for *S. brasiliensis.* Orange patches represent simulated anthropized areas (land-use change), illustrating the potential loss of natural habitat within the climatically suitable zones. The inset map (top left) indicates the study area location within the Caatinga biome, South America

sis occurrence may also be invaded by *Neltuma* spp. (Fig. 2, Table S4). This implies that *S. brasiliensis* may be replaced by *Neltuma* spp. throughout much of the Caatinga.

Discussion

Our results indicate that the potential climatically suitable areas for *S. brasiliensis* estimated by ENMs may be further restricted in the future when anthropization associated with land-cover change (LCC) is taken into account. In addition, regardless of the period or scenario evaluated, the species shows a high potential for spatial overlap with the invasive exotic species *Neltuma* spp. In this context, the combined effects of anthropization and the high degree of overlap with *Neltuma* spp. suggest that the realized distribution of *S. brasiliensis* may be substantially smaller than that estimated based solely on climatic suitability.

Niche models

Although the limited variation in suitability across periods and scenarios observed in the *Neltuma* spp. models could be interpreted as a potential signal of overfitting, this pattern is more parsimoniously explained by model stability rather than by poor generalization. This interpretation is supported by the small differences between TSS values obtained for the training and testing datasets, indicating consistent performance (Table S1). For *S. brasiliensis*, larger discrepancies between training and testing performance were observed in models fitted using the RF algorithm (Table S1), suggesting a higher sensitivity of this algorithm to data structure. However, the influence of this algorithm noise is reduced by the ensemble approach (Hao et al. 2019). Additionally, for both species, the low standard deviation of mean performance across runs indicates high model stability, further supporting the robustness of the modeling framework (Table 2).

Moreover, similarly stable suitability patterns across different time periods and scenarios for *Neltuma* spp. in the Caatinga have been reported in previous studies that adopted comparable methodological decisions, such as the use of globally distributed occurrence records (Heshmati et al. 2019; Pasha and Reddy 2024). This consistency suggests that the observed stability reflects characteristics of the species, such as broad climatic tolerance, rather than a methodological artifact. Likewise, reductions in climatically suitable areas for *S. brasiliensis* under future climate projections have been documented previously (Alves et al. 2020) and are also predicted for other native tree species of the Caatinga (Silva et al. 2019). Taken together, these results indicate that the models exhibit adequate statistical reliability and ecological coherence, allowing for biologically meaningful interpretations.

Given that the variable contributing most strongly to the climatic model of *S. brasiliensis* was Annual Precipitation (Table 3), the projected contractions of suitable areas are likely associated with anticipated changes in the hydrological regime of the Caatinga. Precipitation is widely recognized as the primary factor controlling species distributions in seasonally dry tropical environments, including the Caatinga (Albuquerque et al. 2012; Rito et al. 2017). Additionally, precipitation during the rainy season and isolated showers in the dry season are also closely related to the secondary growth of *S. brasiliensis* (Carvalho et al. 2018). Thus, it is plausible that the reduction of climatically suitable areas for the occurrence of *S. brasiliensis* reflects the predicted decrease in precipitation volume in the

Caatinga in the coming decades (Silva et al. 2023; Torres et al. 2017), especially under the more pessimistic scenarios.

On the other hand, Isothermality was the most important climatic predictor for *Neltuma* spp. (Table 3), indicating that annual thermal stability may play an important role in shaping its potential distribution. As a species that occurs mainly in semi-arid environments (Pasha and Reddy 2024), this pattern is consistent with its ability to tolerate high temperatures (El-Keblawy and Al-Rawai 2005; Sintayehu et al. 2020) and often cannot withstand strong decreases in these (Pasiecznik et al. 2001). Accordingly, the Caatinga exhibits a relatively stable annual temperature range, varying between 25 °C and 30 °C (Sampaio 2003), which favors the occurrence of this species. Such conditions tend to remain in the Caatinga, even under scenarios forecasting increased temperatures due to climate change (Ambrizzi and Araujo 2020), favoring the persistence of suitable areas for *Neltuma* spp., as observed in the climate models.

Anthropization and overlap with *Neltuma* spp

Although ENMs provide valuable insights into areas that are climatically suitable for *S. brasiliensis* and *Neltuma* spp., it is important to recognize that these models represent potential rather than realized occupancy. Actual species distributions are shaped by additional filters, including edaphic conditions, positive and negative biotic interactions, dispersal accessibility, and the evolutionary capacity to adapt to novel environments (Soberón and Peterson 2005). Anthropogenic factors also play a major role in constraining species distributions and should therefore be explicitly considered in ENM based assessments (Frans and Liu 2024). By explicitly accounting for these additional constraints, our study highlights that climatically suitable areas identified by ENMs may not necessarily correspond to areas capable of sustaining viable populations, underscoring the importance of integrating multiple ecological and anthropogenic factors when interpreting model outputs. In agreement with this perspective, using a methodological framework similar to that adopted here, Portela et al. (2023) demonstrated that climatically suitable areas for the native palm *Euterpe edulis* Mart. may be substantially reduced in the future due to vegetation cover loss and declines in disperser richness. Thus, the integrative approach employed in this study provides a more refined understanding of species vulnerability and can support conservation strategies that prioritize both climatically suitable and ecologically viable habitats.

The reduction of suitable areas depicted in the models when considering LCC is consistent with the general characteristics of this process and the known environmental preferences of *S. brasiliensis*. The degradation caused by the replacement of natural environments with anthropized areas can make it difficult or impossible for native species to establish and persist (Fragoso et al. 2017). This is often associated with characteristics commonly observed in anthropic environments, such as low-quality soils (Macedo et al. 2023), absence of dispersers (Wolfe et al. 2019), and intense fragmentation (Holl et al. 2000). The presence of anthropized areas may also hinder species dispersal toward climatically suitable environments (e.g., Selwood et al. 2014). Supporting this interpretation, Ramos et al. (2023), when evaluating the impact of different anthropogenic disturbances (e.g., pasture, agriculture, and urban infrastructure) on plant communities in the Caatinga, found that *S. brasiliensis* occurred only in less impacted and more humid environments, albeit at low abundance. Thus, climatically suitable areas for the occurrence of *S. brasiliensis* that are anthropized

may constrain the realization of its potential distribution and limit access to other suitable areas at the landscape scale. This pattern is particularly concerning given that most projections indicate a continued increase in anthropized areas.

In contrast, for invasive exotic species such as *Neltuma* spp., anthropized environments may represent a window of opportunity, as suggested by previous studies linking anthropogenic disturbance to invasion success. The formation of anthropic environments can lead to the exclusion of potential competitors (Daly et al. 2023), creating vacant niches that allow invasive species to establish and spread (Jauni et al. 2015). Consistent with this, several studies have shown that anthropization has benefited *Neltuma* spp. (Souza Nascimento et al. 2020), facilitating the replacement of native species (Gallaher and Merlin 2010; Edrisi et al. 2020). In the Caatinga, *Neltuma* spp. have demonstrated higher competitive abilities than some native tree species (Souza Nascimento et al. 2014; Oliveira et al. 2017b; Barros et al. 2020). Oliveira et al. (2012) reported that *N. juliflora* seedlings exhibit rapid growth in diameter and height, which may favor faster occupation of vacant niches. This facilitation mediated by anthropogenic activities is widely recognized as an important factor driving invasion success across different ecosystems (Pyšek et al. 2010), including the Caatinga (Pinto et al. 2020).

The vulnerability of *S. brasiliensis* becomes even more concerning in anthropized areas when considering its potential interaction with *Neltuma* spp. When evaluating the effects of the biological invasion of *Neltuma* spp. on the composition and structure of the shrub-tree stratum in a Caatinga area, Pegado et al. (2006) demonstrated that the presence of this species reduced the absolute density of *S. brasiliensis* from 40 individuals per hectare to 2.5. Similarly, Andrade et al. (2009; 2010) reported a negative relationship between the presence of *Neltuma* spp. in the Caatinga and the abundance of some native species, including *S. brasiliensis*. Furthermore, other studies conducted in the Caatinga also found *S. brasiliensis* occurring at lower densities compared to *Neltuma* spp. (Santos and Santos 2012; Fônseca et al. 2016). Considering the competitive exclusion described in the literature, *Neltuma* spp. may represent a potential additional stressor for *S. brasiliensis* in the overlapping areas identified in our results, particularly in landscapes impacted by anthropization.

In non-anthropized environments within the overlapping suitable area between the two species, the probability of *Neltuma* spp. dispersal is lower, since these conserved environments tend to be more resistant to invasion as most niches are occupied (Daly et al. 2023; Le et al. 2023). However, the possibility that this species may disperse into these environments and act as a "dormant invader," waiting for disturbances that could facilitate its expansion, should not be dismissed (Daly et al. 2023). In this context, even the intense extraction pressure suffered by *S. brasiliensis* (Kiill and Lima 2011) may act as a disturbance agent, promoting the invasion process of *Neltuma* spp. Thus, an unforeseen disturbance event not accounted for in our projections could make a conserved area susceptible to invasion by *Neltuma* spp. in the future.

Ecological and socioeconomic impacts of baraúna decline

The likely exclusion of *S. brasiliensis* in some areas, as demonstrated in our models, will also affect other ecological and socio-economic aspects of the Caatinga. During the dry season, characterized by low resource availability in the Caatinga, *S. brasiliensis* serves as an important food source for various floral visitors (Kiill and Lima 2011). Many native bees

also use cavities in its trunks for nesting (Kiill 2011). Additionally, the species is widely used for firewood, charcoal, metallurgical coke, civil construction, agricultural activities, and tool manufacturing (Tigre 1970; Carvalho 2008). Ethnobotanical studies show that *S. brasiliensis* is a key species for many communities in the Caatinga, used for treating coughs, intestinal problems (Agra et al. 2007), fractures, general inflammations (De Albuquerque et al. 2007), verminoses (Almeida et al. 2005), among others (Barreto et al. 2022). Therefore, it is imperative that actions be taken to conserve *S. brasiliensis* and consequently protect the ecological interactions and socio-economic resources mediated by it in the Caatinga.

Methodological limitations and considerations

It is important to recognize that the interpretation of anthropized areas in this study is conditioned by both the spatial scale and the way in which the anthropization variable was constructed. Methodologically, anthropization was defined as the aggregation of agricultural and urban LCC classes, generating a proxy of human influence. After resampling the LCC data to an approximate resolution of 4.5 km, each pixel represents an aggregated land-use signal, within which it is not possible to distinguish different classes, intensities, or spatial configurations of anthropization. Therefore, we did not aim to identify which anthropogenic component was the primary driver, nor to infer specific ecological mechanisms associated individually with agriculture or urbanization. Instead, we present an integrated assessment of the general influence of anthropization, at a regional scale, on the potential distribution of the analyzed species. Accordingly, the detected effects should be interpreted as the combined result of the presence of anthropized environments in the landscape, rather than as homogeneous barriers or opportunities imposed by a single LCC type. Despite the usefulness of this approach for understanding broad-scale patterns, we believe that future studies may evaluate each LCC class separately and provide new perspectives.

Although this study adopted an integrative approach by considering climatic variables, LCC, and biotic interactions (biological invasion), other relevant environmental factors were not explicitly incorporated into the analyses and may contribute to a more refined understanding of the potential distribution of the evaluated species. For example, edaphic variables, such as soil characteristics, as well as indices related to aridity and water availability, can influence species distributions (Silva & Souza 2022). The inclusion of these factors in future studies may allow a more complete characterization of the environmental constraints acting on species, in addition to reducing uncertainties associated with spatial projections. Thus, we expect that future research will address other important factors influencing species distributions.

Conclusion

We conclude that projected changes in climatic suitability indicate that *S. brasiliensis* may experience a substantial reduction in the areas potentially suitable for its occurrence in the Caatinga, particularly under more pessimistic future scenarios. A large part of the remaining suitable areas for the native species may suffer substantial losses due to the proportional increase in anthropization caused by the LCC process in the Caatinga. In addition to this concerning scenario, a high rate of overlap was observed between *S. brasiliensis* and the

invasive exotic species *Neltuma* spp., a factor that may affect the potential distribution of *S. brasiliensis*, especially in anthropized areas. Considering the conservation of *S. brasiliensis* in the Caatinga through the end of the century, we expect that the results of this study may support the selection of climatically suitable areas with a lower likelihood of becoming anthropized due to LCC. Furthermore, it is extremely important that the control of *Neltuma* spp. in the Caatinga be prioritized, aiming especially at the protection of keystone species such as *S. brasiliensis*.

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Author contributions Data collection and preparation were carried out by D.O.R., L.F.R.J.R., and D.A.M. Analyses were performed by D.O.R., with support and suggestions from J.R.F., V.L.-S., R.M.C.P., and L.M.R. The first draft of the manuscript was written by D.O.R., and all authors reviewed and commented on subsequent versions. All authors read and approved the final manuscript. The project was supervised by J.R.F.

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Data availability The data that support this study were derived from the following resources available in the public domain: https://doi.org/10.15468/dl.bhb26j, https://doi.org/10.15468/dl.w7zqxw, http://splink.cria.org.br, and https://www.worldclim.org. The scripts used for the modeling step can be found on the biomod2 package website (https://biomodhub.github.io/biomod2/index.html).

Declarations

Competing interests The authors declare no competing interests.

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