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Climate Change May Increase Environmental Suitability of the Babassu Complex (*Attalea* spp., Arecaceae)

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ABSTRACT

Aim: This study aimed to identify the key bioclimatic factors driving the distribution of the Babassu Complex across the Neotropics in the current scenario (2011–2040), and to project their range shifts under future climate scenarios (2041–2070 and 2070–2100).

Taxon: Babassu Complex (Arecaceae): *Attalea barreirensis*, *A. eichleri*, *A. funifera*, *A. maripa*, *A. phalerata*, *A. speciosa*, and *A. vitrivir*.

Location: Neotropical region.

Methods: We employed Species Distribution Modelling using four algorithms: Maximum Entropy (MaxEnt), Random Forest (RF), Boosted Regression Trees (BRT), and Generalised Linear Models (GLM) for the seven babassu species and for the combined Babassu Complex dataset. GBIF presence-only data was combined with CHELSA 2.1 bioclimatic variables from current and future scenarios to fit the models. Projections for 2041–2070 and 2071–2100 were derived for two high-emission climate scenarios (SSP3 7.0 and SSP5 8.5), using an ensemble of five global climate models.

Results: The RF and BRT algorithms provided more conservative predictions for the current scenario, while MaxEnt and GLM projected broader distributions. Temperature seasonality was the most important suitability predictor. *Attalea maripa*, *A. phalerata*, and *A. speciosa* showed the broadest suitability ranges, while *A. funifera* and *A. vitrivir* were most constrained. Future scenarios projected major suitability increases (up to 871.80% for the Complex under SSP5-8.5 by 2071–2100), particularly in Amazonian and Cerrado regions. Only *A. funifera* and *A. vitrivir* showed declines (−8.55% and −20.97% respectively under SSP3-7.0).

Main Conclusions: We anticipate that climate change may favour babassu species that tolerate warmer and more variable conditions, promoting their expansion. While this may support restoration and livelihoods, unmanaged spread could disrupt local ecosystems. It is recommended that future research focus on incorporating anthropogenic variables, validating predictions with field data, and exploring species-specific ecological responses to climate change.

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1 | Introduction

The Arecaceae family represents one of the largest and most ecologically significant tropical botanical families, contributing to nutrient cycling, providing habitat structure, food, and materials for both biodiversity and local communities (Eiserhardt et al. 2011). Within this family, the genus *Attalea* is recognised as a major component of the Neotropical flora (Freitas et al. 2016; Pintaud 2008). From the c.a. 40 species in the genus, at least seven recognised species and two hybrids form the “Babassu Complex”: *Attalea barreirensis* Glassman, *A. eichleri* (Drude) A.J. Hend, *A. funifera*, *A. maripa* (Aubl.) Mart., *A. phalerata* Mart. ex Spreng., *A. speciosa* Mart. ex Spreng., *A. vitiviv.*, *A. × teixeirana* (Bondar) Zona (a hybrid of *A. eichleri* and *A. speciosa*), and *A. × dahlgreniana* (Bondar) Wess. Boer (a hybrid of *A. speciosa* and *A. maripa*). Known locally as “babassu” or “babaçu,” these palms are predominantly found in tropical countries such as Brazil, Mexico, Bolivia, Colombia, and Suriname (Teixeira 2008; Santos-Filho et al. 2013; Silva et al. 2014; Reis et al. 2018).

The Babassu Complex refers to a group of closely related *Attalea* species that exhibit overlapping morphological traits, frequent natural hybridisation, and unresolved taxonomic boundaries (Cavallari and Toledo 2016; Mata et al. 2022; Pintaud 2008). Although its species share many anatomical features such as uniseriate epidermis, glandular scars, and dorsiventral mesophyll, they also show diagnostic differences in traits like stomatal distribution, vascular bundle organisation, and palisade parenchyma layers (Mata et al. 2022), justifying their recognition as distinct taxa and supporting species-level ecological assessment.

From an ecological perspective, babassu palms are foundational species that influence forest structure, microclimate regulation, nutrient cycling, and soil stabilisation across various Neotropical biomes (see Araújo et al. 2016; Corrêa et al. 2023; Porro 2019; Ressorio et al. 2024). Socioeconomically, they support the livelihoods of traditional communities (Almeida Campos et al. 2015; Lima et al. 2003), such as the communities of babassu coconut breakers, women who rely on artisanal harvesting and processing of its fruit given their broad range of uses (De Oliveira et al. 2022; Mitja et al. 2019; Porro et al. 2011; Shiraishi Neto 2017). These species can be utilised for handicrafts, construction, and human consumption. The babassu species provide a diverse range of products; the babassu nuts are the most prominent, which have the potential to be processed into various by-products with different levels of processing complexity, including mesocarp flour (Cardoso Vieira et al. 2023), oil (Neto et al. 2021), adsorptive material for chemical molecules (Vieira et al. 2011), biofuel, charcoal (Corrêa et al. 2023), and animal feed (Portela et al. 2024).

Comprehension of the ecological dynamics and distribution patterns of babassu is, therefore, imperative to ensure the sustainability of such socio-ecological systems and to support conservation and spatial planning efforts across the Neotropics. Climatic variables are especially relevant for palms, whose distributions are often closely tied to thermal and moisture regimes (De Kort et al. 2021; Eiserhardt et al. 2011; Peterson et al. 2011). While variables such as water availability and temperature

seasonality are recognised as key determinants for many tropical palms (Kissling et al. 2011) the specific climatic thresholds that shape the distribution of babassu species remain unresolved.

As a powerful tool in conservation biogeography, the emergence of Species Distribution Modelling (SDM) has been instrumental in bridging knowledge gaps related to the geographic distribution of species and identifying species–climate relationships (Elith and Franklin 2013; Guisan and Thuiller 2005; Guisan and Zimmermann 2000), encompassing historical biogeography, diversity patterns, ecosystem conservation, and the impacts of climate change (Brun et al. 2020; Franklin 2023; Freer et al. 2018; Maltby et al. 2020; Volis and Tojibaev 2021). The employment of advanced SDM techniques, involving bioclimatic variables and multiple algorithms, furnishes valuable insights into species distributions and potential niche shifts under prevailing and future climate scenarios (Alves et al. 2019; Brun et al. 2020; Katuwal et al. 2023; Valavi et al. 2022). This is of particular importance for palms and their pivotal ecological roles in tropical ecosystems and economic importance for local communities (Blach-Overgaard et al. 2010; Costa et al. 2022; Mitja et al. 2019).

Previous SDM studies have assessed the climatic suitability of *Attalea* species. Menezes et al. (2023) projected future distributions of *A. pindobassu* in the Brazilian biome Caatinga under the scenarios SSP2-4.5 and SSP5-8.5, finding drastic losses of suitable habitat, especially under pessimistic scenarios. Likewise, De Lima et al. (2022) modelled 15 palm species in the Atlantic Forest, including *A. dubia* (Mart.) Burret and *A. humilis* Mart. Ex Spreng., revealing conservation gaps and spatial mismatches between suitable habitats and protected areas. However, no comprehensive multi-species SDM has been conducted for the Babassu Complex. These previous efforts have either focused on single species or specific regions, limiting their relevance for broader-scale conservation and land-use planning, which represents a critical gap. The lack of spatially explicit, climate-based assessments at the group level hinders our ability to anticipate range shifts, identify conservation priorities, and develop adaptation strategies under climate change.

Given their ecological dominance, socioeconomic importance, and biogeographic significance, the Babassu Complex is a high-priority group for climate impact assessments. Thus, the objective of this study is to identify the key bioclimatic factors driving the distribution of the Babassu Complex and its species across the Neotropical region, and project their range shifts under future climate scenarios (SSP3-7.0 and SSP5-8.5) across two periods (2041–2070 and 2071–2100), thereby contributing to a more nuanced understanding of their vulnerability and resilience in a changing climate.

2 | Material and Methods

2.1 | Data Collection

This study focused on species distribution modelling (SDM) for the seven species of the *Attalea* genus identified as part of the Babassu Complex and for the combined dataset. The species selection was based on their taxonomic inclusion in the Babassu Complex, supported by anatomical and morphological evidence

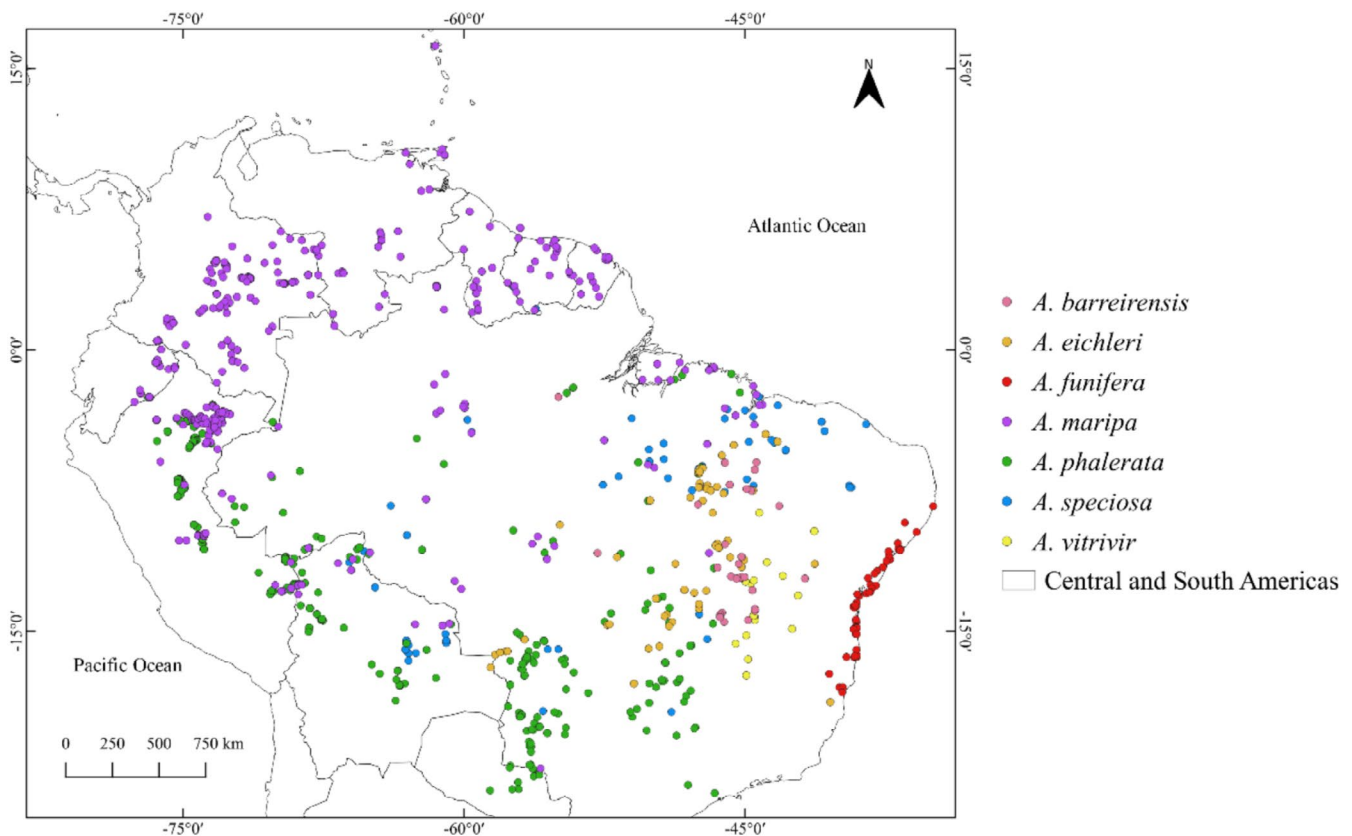


FIGURE 1 | Distribution map of occurrence points obtained from the GBIF database for the Babassu Complex species: *A. phalerata* ($n = 15,170$), *A. maripa* ($n = 3580$), *A. eichleri* ($n = 142$), *A. speciosa* ($n = 129$), *A. funifera* ($n = 84$), *A. barreirensis* ($n = 52$), and *A. vitrivir* ($n = 47$).

(Cavallari and Toledo 2016; Mata et al. 2022), the availability of sufficient georeferenced occurrence data for ecological modeling, and their ecological and socioeconomic importance across the region. Presence-only occurrence data were obtained from the Global Biodiversity Information Facility (GBIF) database, totalling 19,204 records distributed among species as follows: *A. phalerata* ($n = 15,170$), *A. maripa* ($n = 3580$), *A. eichleri* ($n = 142$), *A. speciosa* ($n = 129$), *A. funifera* ($n = 84$), *A. barreirensis* ($n = 52$), and *A. vitrivir* ($n = 47$) (Figure 1).

To minimise spatial sampling bias, duplicate and spatially clustered occurrences were filtered from the dataset so that only one occurrence per 20 km grid cell was retained. This filtering procedure was used to reduce the influence of highly sampled clusters, often associated with accessible or well-surveyed areas, while preserving broader landscape-level occurrence patterns (Lake et al. 2020; Lee et al. 2022). After filtering, the number of retained occurrence points per species was: *A. barreirensis* ($n = 41$), *A. eichleri* ($n = 79$), *A. funifera* ($n = 65$), *A. maripa* ($n = 570$), *A. phalerata* ($n = 431$), *A. speciosa* ($n = 84$), *A. vitrivir* ($n = 27$), and the combined dataset ($n = 1269$).

2.2 | Bioclimatic Variables

For both current and future scenarios, bioclimatic variables were sourced from the Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA) database, version 2.1 (Table S1.2), which incorporates orographic corrections (e.g., wind fields, valley exposure) to enhance the accuracy of

temperature and precipitation estimates in complex terrains (Brun et al. 2022; Karger et al. 2017, 2020, 2021). Each variable was obtained as a georeferenced TIFF file (GeoTIFF) with an original resolution of 30 arc-second ($\sim 1 \text{ km}^2$), using a geographic coordinate system referenced to the WGS 84 horizontal datum.

The predictor variables employed to model the current climate scenario covered the baseline period of 2011–2040. For future scenarios, the bioclimatic predictors were obtained from the *Scenario Model Intercomparison Project* (SMI), part of the *Coupled Model Intercomparison Project Phase 6* (CMIP6), accessed via the CHELSA V2.1 database. We considered two Shared Socioeconomic Pathways (SSPs) of high greenhouse gas emission: SSP3 7.0 and SSP5 8.5, and two time periods: 2041–2070 and 2071–2100. These scenarios were chosen to represent upper-bound climate change trajectories relevant for ecological risk assessments and stress-testing conservation planning. While recent studies have questioned the global plausibility of SSP5-8.5 due to evolving energy and policy trends (Hausfather and Peters 2020; Scafetta 2023), both SSP3-7.0 and SSP5-8.5 remain valuable for identifying potential biodiversity impacts in regions where mitigation policies are less consistent or delayed, such as parts of the Neotropics. SSP3-7.0 assumes a fragmented world with low international cooperation, while SSP5-8.5 represents a fossil-fuelled development trajectory with high energy demand (Riahi et al. 2017). In this context, these scenarios were not used as predictions, but as boundary conditions to explore the vulnerability and resilience of the Babassu Complex under contrasting high-risk futures. The projections were based on all five Global Climate Models (GCMs) available in the CHELSA

database: National Oceanic and Atmospheric Administration—Geophysical Fluid Dynamics Laboratory (GFDL-ESM4), Met Office Hadley Centre (UKESM1-0-LL), Max Planck Institute for Meteorology (MPI-ESM1-2-HR), Institut Pierre Simon Laplace (IPSL-CM6A-LR), and Meteorological Research Institute (MRI-ESM2-0).

2.3 | Pre-Processing and Modelling

The occurrence of palms has been primarily observed in tropical regions (Eiserhardt et al. 2011); moreover, the distribution of babassu species appears to be centred in the Neotropics (Teixeira 2008; Santos-Filho et al. 2013; Silva et al. 2014; Reis et al. 2018). Thus, all models were generated for the Neotropical region, encompassing Central and South America and the Caribbean. The SDMs were implemented using an integration of the *sdm* (Naimi and Araújo 2016) and *dismo* (Hijman et al. 2024) packages in R 4.3.2. The models were trained using 70% of the retained occurrence points, with the remaining 30% being allocated for model testing.

Species distribution models based on presence-only data rely on recorded occurrences and do not account for confirmed absences. To compensate, researchers have employed various strategies to refine model predictions and improve ecological inference, such as the use of background points (Renner et al. 2015). To minimise sampling bias and act as ‘pseudo-absence’ data in the models, ten thousand background points were randomly generated across the Neotropical region, which corresponds to the biogeographic extent of the Babassu Complex and reflects the broad ecological amplitude of the *Attalea* genus. This number is frequently recommended in SDMs studies to ensure sufficient environmental coverage while maintaining computational efficiency (Radomski et al. 2022; Valavi et al. 2022; Whitford et al. 2024). The selection of background points in SDMs varies considerably (Steen et al. 2024; Whitford et al. 2024), and it is well known that using large background extents can inflate environmental gradients and potentially compromise model realism, particularly for species with narrow distributions and few occurrence records (Vasquez et al. 2021). In our case, species such as *A. vitivir* ($n = 27$) and *A. barreirensis* ($n = 41$) are restricted in space (see Figure 1), which could increase sensitivity to this issue. However, because no detailed information exists on their climatic tolerances or dispersal constraints, defining a more ecologically precise background would be speculative. As such, the Neotropical background was retained for all species to maintain consistency and support comparative and ensemble analyses. Moreover, benchmark studies show that presence-background models can still achieve reliable performance for rare species, provided that background points are well-distributed and model complexity is appropriately managed (Valavi et al. 2022; Whitford et al. 2024). Our approach thus seeks to balance ecological realism and methodological consistency, while acknowledging the limitations of modelling poorly known and geographically restricted species.

Multicollinearity is a common issue in ecological modelling, as it complicates the estimation of variable effects and reduces model extrapolation accuracy (Brun et al. 2020; Graham 2003). To address this, a multicollinearity analysis was conducted

(Dormann et al. 2013) for the seven species and Babassu Complex overall, using all the bioclimatic variables considered for constructing the bioclimatic models. Variance inflation factors (VIF) were calculated using the *vifstep* function from the *usdm* package (Naimi et al. 2014), utilising default specifications, with variables showing $VIF > 10$ considered highly collinear and excluded to prevent overfitting.

Given the unavailability of evapotranspiration and vapour pressure deficit data for future climate scenarios in the CHELSA database, a correlation analysis was conducted utilising Spearman's coefficient (See Figure S1.1) on the complete set of current bioclimatic variables. This analysis, performed with the *rcorr* function from the *Hmisc* package (Hijman et al. 2024), identified the most strongly correlated variables to substitute for missing predictors. To avoid redundancy, each missing predictor was replaced only by its single most correlated variable, ensuring that a given predictor was not associated with multiple replacements. All the remaining predictors used for current and future scenarios can be found in Table S1.3. For the current scenario, multicollinearity analysis resulted in 8–12 variables being kept in model formulations. The most frequently retained predictors included mean diurnal temperature range (MDTR), mean monthly precipitation amount of the warmest quarter (MMPAWaQ), mean daily mean air temperatures of the wettest quarter (MDTWaQ), and precipitation amount of the wettest month (PAWM), which appeared in at least seven of the eight models (Figure S1.2). Conversely, annual precipitation amount (APA) (*A. speciosa* model), mean monthly potential evapotranspiration (PPMean) (*A. eichleri* model), mean monthly vapour pressure deficit (VPDMean) (*A. funifera* model), and mean daily mean air temperatures of the driest quarter (MDTDQ) (*A. maripa* and *A. phalerata* models) were less frequently selected.

To generate the SDMs for all the datasets in current and future scenarios, models were implemented using the *sdm* package, employing four algorithms with complementary modelling approaches: Boosted Regression Trees (BRT) (Friedman 2001), Generalised Linear Models (GLM) (McCullagh and Nelder 1989), Maximum Entropy (MaxEnt) (Phillips et al. 2006) and Random Forest (RF) (Breiman 2001). These algorithms were chosen because they represent a diverse spectrum of statistical and machine learning methods, ranging from parametric (GLM), semi-parametric (MaxEnt), to non-parametric (BRT, RF), and are widely benchmarked in ecological niche modelling (Norberg et al. 2019; Qiao et al. 2019; Shabani et al. 2016). This diversity helps capture varying species–environment relationships while mitigating algorithm-specific biases in ensemble predictions (Valavi et al. 2022). To evaluate the mean performance of the algorithms, the k-fold cross-validation technique was implemented through the *sdm* function from the *sdm* R package. In this process, the occurrence data were divided into five folds, and the cross-validation procedure was repeated five times. This approach yielded 25 models (5 folds $\times$ 5 repetitions) per species–algorithm combination, thereby providing a robust assessment of model performance, utilising multiple random partitions as opposed to a single one (Phillips et al. 2006). The performance of the models was evaluated using the receiver operating characteristic (ROC) curve (Phillips et al. 2006), assessed based on area under the curve (AUC) values (Swets 1988),

True Skill Statistics (TSS) (Allouche et al. 2006), and deviance measures. AUC or TSS values of 1 indicate perfect predictive performance, while values of ≤ 0.5 suggest random prediction (Allouche et al. 2006; Swets 1988). According to these metrics, all models showed good performance (AUC: 0.95–1.00; TSS: 0.85–0.99; Deviance: 0.08–0.37; Table S1.4a–c).

To assess the contribution of individual variables to the presence-absence of Babassu Complex species, we calculated relative variable importance (IR%), based on the mean AUC metric as implemented in the R package *sdm* (Naimi and Araújo 2016). These values were then visualised using the *getVarImp* function. Both model performance metrics and IR% values are available in the metadata of the SDM objects.

2.4 | Habitat Suitability and Presence-Absence Maps

Habitat suitability maps were generated for each of the four modelling algorithms (MaxEnt, RF, GLM, and BRT), for each individual species and for the Babassu Complex overall, using the *predict* function from the *dismo* package. For the current scenario (2011–2040), an ensemble suitability map was created by integrating the outputs from the four algorithms using a weighted average based on TSS performance criteria (Boali et al. 2024; Marmion et al. 2009). This ensemble approach balances interpretability and predictive power, following best practices for ecological forecasting, and ensures that better-performing models contribute more heavily to the final prediction (Valavi et al. 2022). For the future scenarios (2041–2070 and 2071–2100) under both SSP3-7.0 and SSP5-8.5, the ensemble suitability maps for each species and the Babassu Complex were generated by combining all individual model outputs (i.e., all four algorithms across each of the five GCMs) into a single ensemble per scenario for the period, using TSS-weighted averages. All GCMs (GFDL-ESM4, UKESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0) were given equal representation, but individual model contributions were weighted by algorithmic performance (TSS). This method reflects ensemble modelling practices recommended for ecological forecasting under climate change, helps mitigate model-specific biases, and offers a pragmatic balance between robustness and interpretability (Brun et al. 2020).

The resulting ensemble habitat suitability map for all scenarios was then transformed into binary presence-absence maps, delineating the potential distribution of the seven individual species and the Babassu Complex. This was achieved using the maximum thresholding method (*maxSSS*), which optimises the trade-off between sensitivity (true positive rate) and specificity (false positive rate) and is not affected by the use of pseudo absences (Liu et al. 2013).

Finally, the ensemble maps for both current and future scenarios were reprojected to a Universal Transverse Mercator (UTM) coordinate system and resampled to a spatial resolution of 1 km to allow area calculations and to assess the change in suitable area between classes across scenarios. The suitability maps were classified into four categories: unsuitable (suitability ≤ 0.05), low suitability ($0.05 < \text{suitability} \leq 0.33$), medium

suitability ($0.33 < \text{suitability} \leq 0.66$), and high suitability (suitability > 0.66). The cutoff for unsuitability corresponds to the lower 5th percentile of predicted suitability values, excluding areas environmentally equivalent to background conditions (Almpanidou et al. 2016; Liu et al. 2013). The thresholds for low and medium suitability follow widely used ENM classifications and represent a gradient of environmental favourability (Jiménez-Valverde 2014). Low suitability includes marginal habitats, often corresponding to the lower quantiles of predicted suitability (Liu et al. 2013; Sillero 2011), while medium suitability includes suboptimal but viable environments for species persistence, consistent with transitional habitat categories in SDM frameworks (Franklin 2010). High suitability reflects optimal conditions, defined here as the upper tercile (> 0.66) of predictions based on robust threshold-selection methods (Liu et al. 2016) and aligning with core climatic niches in Neotropical species distributions (Costa et al. 2022). For the current scenario, area calculations were conducted independently for each of the following algorithms: BRT, GLM, MaxEnt, and RF, in addition to the ensemble map. For future scenarios, area calculations were performed for each emission scenario (SSP3 7.0 and SSP5 8.5) across distinct periods (2041–2070 and 2071–2100) for the ensembles only. A detailed methodological workflow is provided in a flowchart (See Figure S1.3). All image processing and map generation were conducted using QGIS Desktop 3.18.2 and R 4.3.2.

3 | Results

3.1 | Relative Importance of Variables

Most variables demonstrated low importance across the majority of SDMs and models (Table S1.5a–h). Results varied significantly among SDMs, resulting in high standard deviations in the mean importance per predictor ($n = 100$) and, consequently, high coefficients of variation. The highest mean Im% values were observed for GLM, while the lowest were found for RF.

Among all predictors, temperature seasonality (TS) emerged most frequently as the variable with the highest Im%, showing a notable association with the distribution of *A. barreirensis* (53.0%), *A. eichleri* (43.6%), *A. maripa* (20.6%), and the Babassu Complex overall (34.5%). Furthermore, *A. eichleri* exhibited robust responses to the annual range of monthly vapour pressure deficit (VPDrange) and mean monthly vapour pressure deficit (VPDmean), *A. speciosa* to isothermality (Iso), and *A. vitrivir* to minimum monthly potential evapotranspiration (PPmin) and precipitation amount of the driest month (PADM).

3.2 | Predicted Current Habitat Suitability and Potential Distribution of the Babassu Complex

The spatial distribution of habitat suitability areas was found to be consistent across SDM predictions (Figure 2a–h), with variations primarily observed in suitability levels (Table S1.6). The GLM algorithm identified the largest areas of high habitat suitability across models (See Table S1.7), while BRT predicted the smallest high-suitability areas but the most extensive

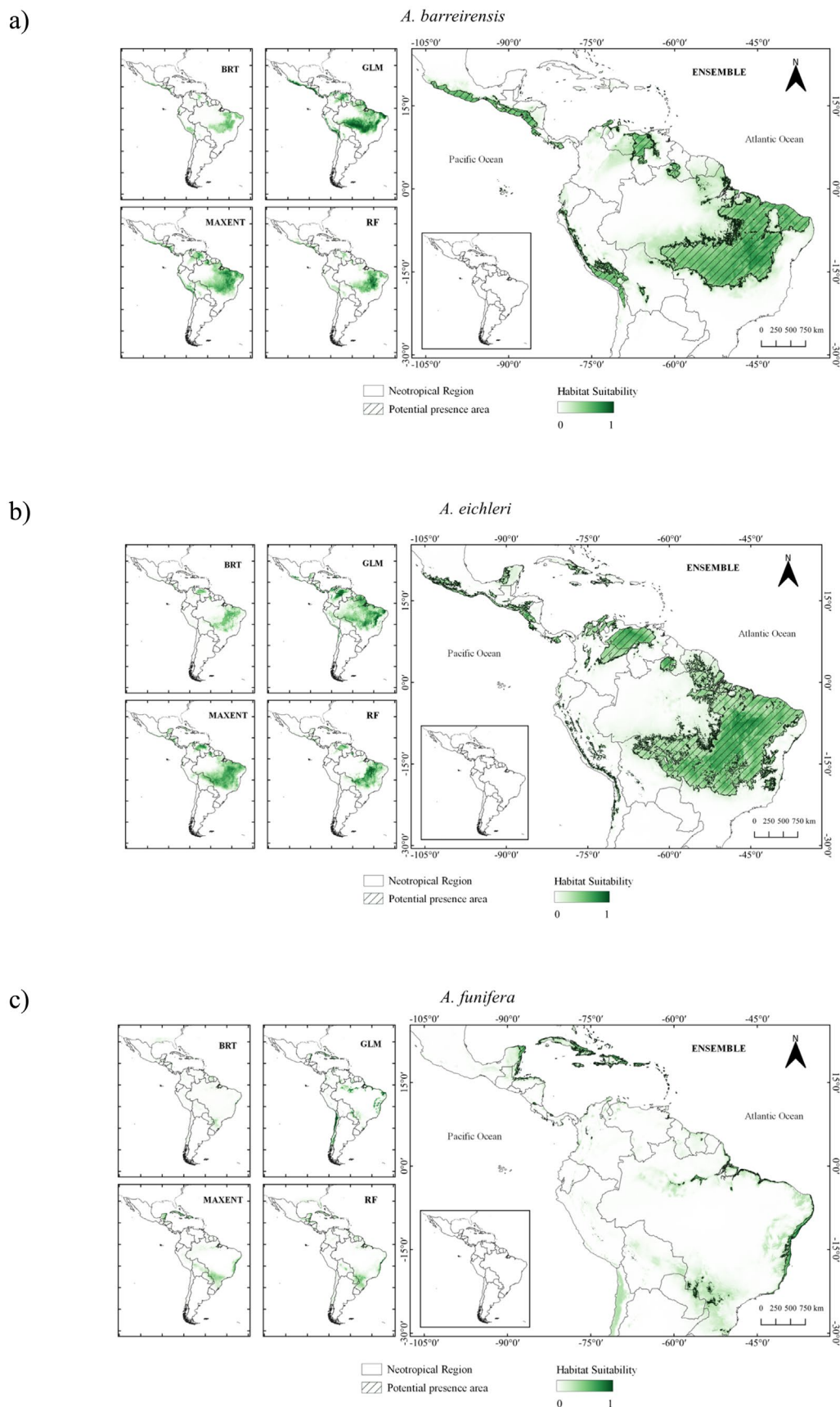


FIGURE 2 | Habitat suitability maps for the modelled distribution of species within the Babassu Complex, based on Maximum Entropy (Maxent), Random Forest (RF), Boosted Regression Trees (BRT), Generalised Linear Models (GLM), and the ensemble map of all algorithms. The maps represent: (a) *A. barreirensis*, (b) *A. eichleri*, (c) *A. funifera*, (d) *A. maripa*, (e) *A. phalerata*, (f) *A. speciosa*, (g) *A. vitrivir*, and (h) the Babassu Complex overall, covering Neotropical region.

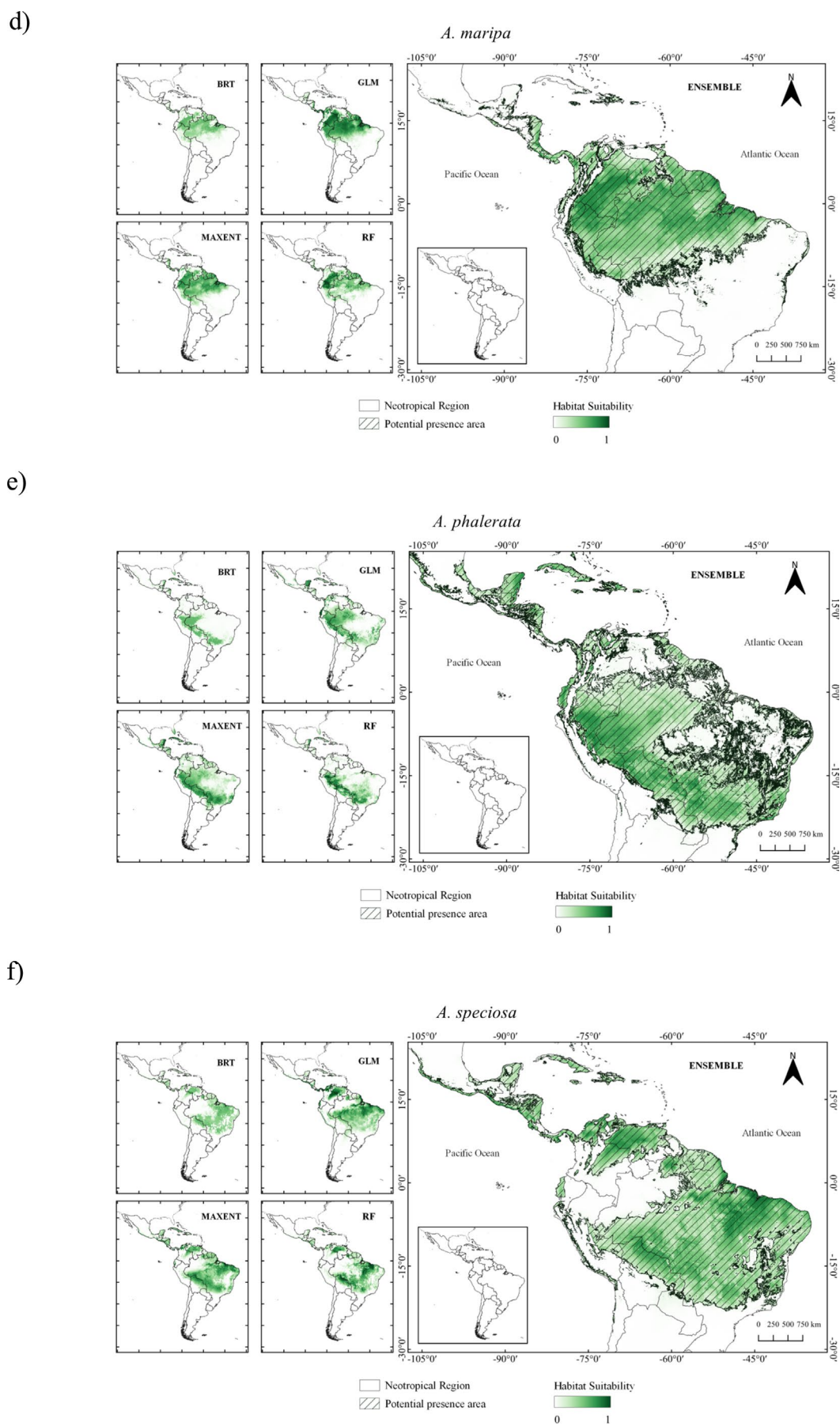
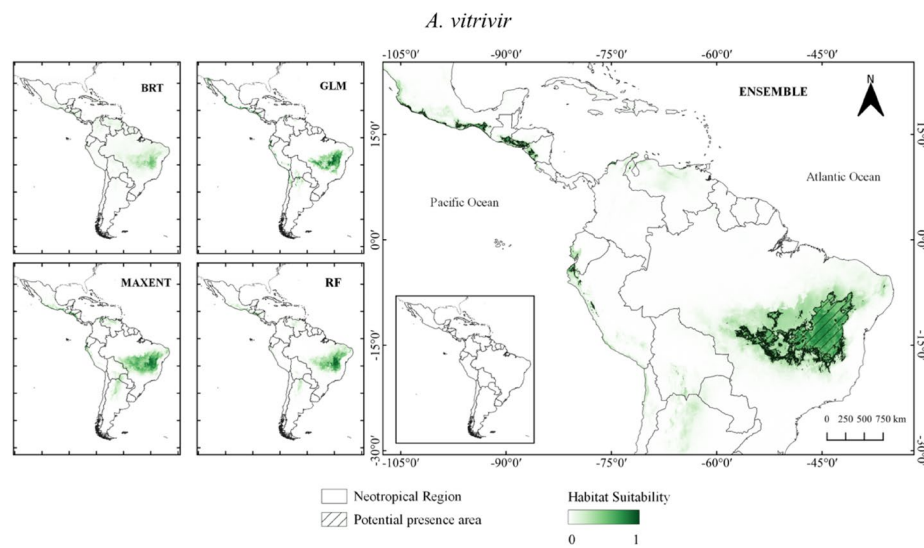


FIGURE 2 | (Continued)

g)



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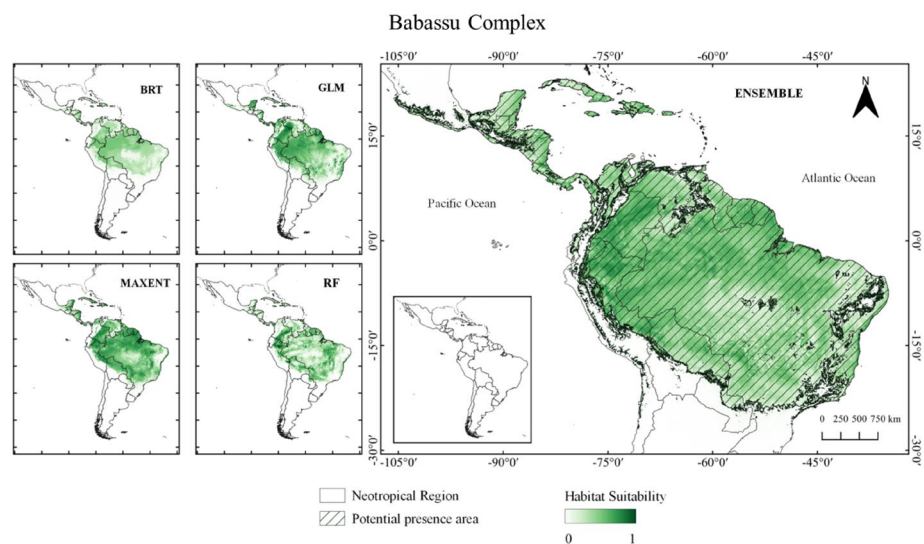


FIGURE 2 | (Continued)

low-suitability regions, with a maximum suitability value of approximately 0.53. RF and BRT models had the most conservative estimates of habitat suitability for the babassu species, while MaxEnt and GLM projected broader areas in the medium and high suitability classes.

Among species, *Attalea speciosa* and *A. maripa* had the largest high-suitability areas, covering 927,503 km² and 915,496 km², respectively. Conversely, *A. vitrivir* (14,502,398 km²) and *A. funifera* (14,020,351 km²) had the most extensive unsuitable areas. For the Babassu Complex as a whole, the most extensive suitability class was medium suitability, covering 7,891,228 km².

3.3 | Changes in Habitat Suitability in Future Climatic Change Emissions Scenarios

The application of SDMs has revealed notable differences in the bioclimatic suitability of species from the Babassu

Complex under current climate conditions, which have demonstrated significant adaptability across tropical regions of the Americas and the Caribbean, particularly in the Amazon rainforest and Cerrado (Figure 2a–h). At the species level, *A. barreirensis* and *A. eichleri* predominantly occupied savanna regions, including the Brazilian Cerrado and the Venezuelan Llanos. *A. funifera* exhibited the most restricted distribution, mainly within the tropical and subtropical moist broadleaf forests of the Brazilian Atlantic Forest, coastal Bahia, and the Brazil-Paraguay border, as well as parts of the tropical and subtropical dry broadleaf forests of the Caribbean and Central America. *A. maripa* showed an intrinsic relationship with the Amazon rainforest in northern South America. *A. phalerata* was found in tropical and subtropical moist forests, flooded grasslands of the Chaco and Pantanal, and savanna regions. Of all the species, *A. speciosa* demonstrated the largest potential distribution, encompassing transitional zones between the Cerrado and Amazon, adjacent areas, and savanna regions across the Americas (Cerrado, Llanos) and the Caribbean. Finally, *A. vitrivir* exhibited one of the smallest

distribution areas, being confined to the Brazilian Cerrado and the transition zones between the Cerrado, Caatinga, and Atlantic Forest.

The analysis revealed that the prediction maps generated by each of the algorithms, and when averaged together, indicated the Babassu Complex as having extensive potential to support its presence across South America. The areas of highest environmental suitability were found to be predominantly concentrated in the northwestern regions of the continent, significantly overlapping the Amazon rainforest. However, a substantial portion of these suitable areas was also identified within the Cerrado biome, indicating a potential intrinsic relationship with both ecosystems.

Comparison of habitat suitability areas between current and future scenarios (see Table 1 and Figure S1.4) indicates a substantial increase in high-suitability areas for most models and climate change scenarios, with the only reductions being observed in the 2071–2100/SSP3 scenario for *A. funifera* (−8.55%) and *A. vitrivir* (−20.97%). The scenario with the most significant increase in high-suitability areas for the majority of models was 2041–2070/SSP3 (Figure 3). For the Babassu Complex, the largest increases in high-suitability areas were recorded across all future scenarios, ranging from 680.78% in 2041–2070/SSP3 to 871.80% in 2071–2100/SSP5.

4 | Discussion

The selection of specific predictors, as observed for annual precipitation amount (APA) (*A. speciosa*), mean evapotranspiration (PPMean) (*A. eichleri*), mean vapour pressure deficit (VPDMean) (*A. funifera*), and mean daily temperature in the driest quarter MDTDQ (*A. maripa* and *A. phalerata*), may indicate more species-specific environmental preferences (Brun et al. 2020; Dormann et al. 2013; Graham 2003). However, it is important to note that the retention of these predictors does not necessarily imply a direct ecological response (Graham 2003), underscoring the need for complementary field and physiological studies to validate these predictors' ecological significance.

The Relative Variable Importance (Im%) values demonstrated that humidity-related variables were not the most influential in modelling Babassu Complex distributions. Instead, temperature seasonality (TS), defined as the standard deviation of mean monthly temperature, exhibited a high retention frequency across species after multicollinearity removal and had the highest Im% values, identifying it as a key predictor. These results corroborate Eiserhardt et al. (2011), who emphasised palm species' sensitivity to cold and seasonal climates due to limited frost tolerance and dormancy mechanisms. These findings serve to reinforce the notion of the pronounced temperature sensitivity exhibited by palms and their marked preference for tropical climates (Eiserhardt et al. 2011).

Concerning SDMs, Generalised Linear Models (GLMs) have been shown to assign higher Im% values to individual bioclimatic variables in comparison to alternative modelling methods. In the context of GLMs, the occurrence of species is

assumed to be associated with environmental variables according to a predefined relationship, thereby placing greater emphasis on variables that exhibit strong statistical associations. This sensitivity may result in an overemphasis on certain predictors, potentially reducing the reliability of species distribution projections and highlighting the importance of ensemble models (Hao et al. 2019; Marmion et al. 2009; McCullagh and Nelder 1989). Conversely, Random Forest (RF) assigned lower numerical importance to individual predictors. This is because RF is a non-parametric algorithm based on an ensemble of decision trees, which distributes variable importance across multiple trees (Antoniadis et al. 2021; Breiman 2001; Zhang et al. 2019). Consequently, RF tends to yield more balanced variable importance values, which are often lower than those observed in parametric models such as GLMs.

The broad suitability ranges exhibited by *Attalea maripa*, *A. phalerata*, and *A. speciosa* suggested high levels of tolerance to present-day bioclimatic conditions, which highlights the necessity for their management. In contrast, the more limited suitability zones of *A. funifera* and *A. vitrivir*, particularly the latter, indicate higher vulnerability to environmental fluctuations. This emphasises the necessity for the formulation of targeted conservation strategies to ensure the continued viability of these species in the context of climate change (Elliott et al. 2024; Lannuzel et al. 2021; Volis and Tojibaev 2021). The use of a uniform Neotropical background extent for all species, including range-restricted taxa like *A. funifera*, *A. barreirensis*, and *A. vitrivir*, ensured methodological consistency and allowed comparative ensemble modelling. However, this approach may overestimate bioclimatic suitability for narrowly distributed species by incorporating ecologically irrelevant areas. While justified by limited ecological information on these species, future studies should explore species-specific extents based on dispersal capacity and biogeographic context to refine predictions (Vasquez et al. 2021; Whitford et al. 2024).

The variations observed among models in the current scenario are indicative of the inherent characteristics of the algorithms used, thus reinforcing the necessity for complementary approaches to enhance projection robustness and minimise methodological uncertainties. These differences arise from the way each algorithm processes environmental information. RF and BRT likely emphasised strong environmental signals and interactions within the training data, constraining their projections to regions with highly suitable conditions while prioritising complexity and precision (Antoniadis et al. 2021; Breiman 2001; Friedman 2001; Zhang et al. 2019). Conversely, MaxEnt and GLM, with their broader statistical assumptions, projected larger continuous areas of medium to high suitability, potentially incorporating marginally suitable regions (Guisan and Zimmermann 2000; McCullagh and Nelder 1989; Phillips et al. 2006).

Furthermore, the ensemble modelling framework combined parametric (GLM), semi-parametric (MaxEnt), and non-parametric (BRT, RF) algorithms to leverage complementary strengths: GLMs provided interpretable relationships between predictors and responses but often produced inflated variable importance values due to model assumptions, while machine-learning methods captured complex interactions and

TABLE 1 | Projected changes in habitat suitability for *A. barreirensis*, *A. eichleri*, *A. funifera*, *A. maripa*, *A. phalerata*, *A. speciosa*, *A. vitivivir*, and the Babassu Complex overall, under SSP3-7.0 and SSP5-8.5 Scenarios (2041–2100 and 2071–2100).

Scenarios									
2041–2070				2071–2100					
SSP3–7.0		SSP5–8.5		SSP3–7.0		SSP5–8.5		SSP3–7.0	
Species	Class	Future (km ²)	Relative Difference (%)	Future (km ²)	Relative Difference (%)	Future (km ²)	Relative Difference (%)	Future (km ²)	Relative Difference (%)
<i>A. barreirensis</i>	Unsuitable	10,389,998	–12.78	11,222,328	–5.79	10,599,801	–11.02	9,662,624	–18.89
	Low	7,550,859	16.80	7,037,553	8.86	8,265,168	27.85	8,340,284	29.01
	Medium	2,922,591	–1.32	2,547,970	–13.97	2,255,124	–23.86	2,898,266	–2.14
	High	710,311	178.68	765,908	200.49	453,666	77.99	672,586	163.88
<i>A. eichleri</i>	Unsuitable	10,203,525	0.14	9,851,437	–3.31	10,266,276	0.76	9,234,843	–9.37
	Low	6,931,939	–17.64	7,564,985	–10.11	7,192,470	–14.54	8,121,934	–3.50
	Medium	2,990,210	13.09	2,956,637	11.82	3,092,123	16.95	2,954,888	11.76
	High	1,448,086	319.90	1,200,700	248.17	1,022,890	196.61	1,262,094	265.97
<i>A. funifera</i>	Unsuitable	4,114,133	–70.66	6,004,479	–57.17	6,964,763	–50.32	4,544,225	–67.59
	Low	16,657,799	133.94	15,181,583	113.21	14,352,789	101.57	16,447,072	130.98
	Medium	764,255	81.03	351,878	–16.65	227,706	–46.06	535,694	26.89
	High	37,572	20.56	35,819	14.93	28,501	–8.55	46,769	50.06
<i>A. maripa</i>	Unsuitable	9,145,010	–22.61	9,146,797	–22.60	8,997,537	–23.86	8,997,711	–23.86
	Low	5,799,128	25.04	5,650,332	21.83	5,878,972	26.76	5,713,825	23.20
	Medium	4,334,464	2.63	4,524,891	7.14	4,608,890	9.13	4,573,014	8.28
	High	2,295,158	150.70	2,251,740	145.96	2,088,360	128.11	2,289,209	150.05
<i>A. phalerata</i>	Unsuitable	5,762,009	–25.74	6,098,864	–21.40	5,855,616	–24.53	6,262,523	–19.29
	Low	7,905,634	–20.43	8,162,661	–17.84	8,303,156	–16.43	6,851,348	–31.04
	Medium	5,847,963	84.71	5,519,804	74.35	5,729,364	80.97	6,509,678	105.61
	High	2,058,153	180.65	1,792,430	144.41	1,685,624	129.85	1,950,210	165.93

(Continues)

TABLE 1 | (Continued)

Scenarios												
2041–2070						2071–2100						
Species	Class	SSP3–7.0			SSP5–8.5			SSP3–7.0			SSP5–8.5	
		Future (km²)	Relative Difference (%)	Future (km²)	Relative Difference (%)	Future (km²)	Relative Difference (%)	Future (km²)	Relative Difference (%)	Future (km²)	Relative Difference (%)	
<i>A. speciosa</i>	Unsuitable	6,270,546	−33.72	7,329,885	−22.52	7,834,524	−17.19	7,098,530	−24.97			
	Low	7,670,282	16.46	7,065,532	7.28	7,171,222	8.89	7,443,843	13.03			
	Medium	5,073,102	9.80	5,042,139	9.13	5,321,250	15.17	4,859,595	5.18			
	High	2,559,830	175.99	2,136,203	130.32	1,246,764	34.42	2,171,792	134.15			
<i>A. vitrivir</i>	Unsuitable	12,884,926	−11.15	12,859,357	−11.33	13,861,406	−4.42	13,051,311	−10.01			
	Low	7,484,122	28.60	6,857,590	17.84	6,962,269	19.63	6,860,189	17.88			
	Medium	954,730	−12.12	1,562,079	43.79	603,198	−44.47	1,435,779	32.17			
	High	249,982	34.50	294,734	58.58	146,886	−20.97	226,480	21.86			
Babassu Complex	Unsuitable	6,188,662	−17.12	6,515,732	−12.75	6,032,378	−19.22	6,087,909	−18.47			
	Low	4,050,732	−30.26	4,004,980	−31.05	4,030,283	−30.61	4,009,590	−30.97			
	Medium	7,997,410	1.35	7,431,489	−5.83	7,547,891	−4.35	7,322,919	−7.20			
	High	3,336,956	680.78	3,621,558	747.37	3,963,208	827.31	4,153,342	871.80			

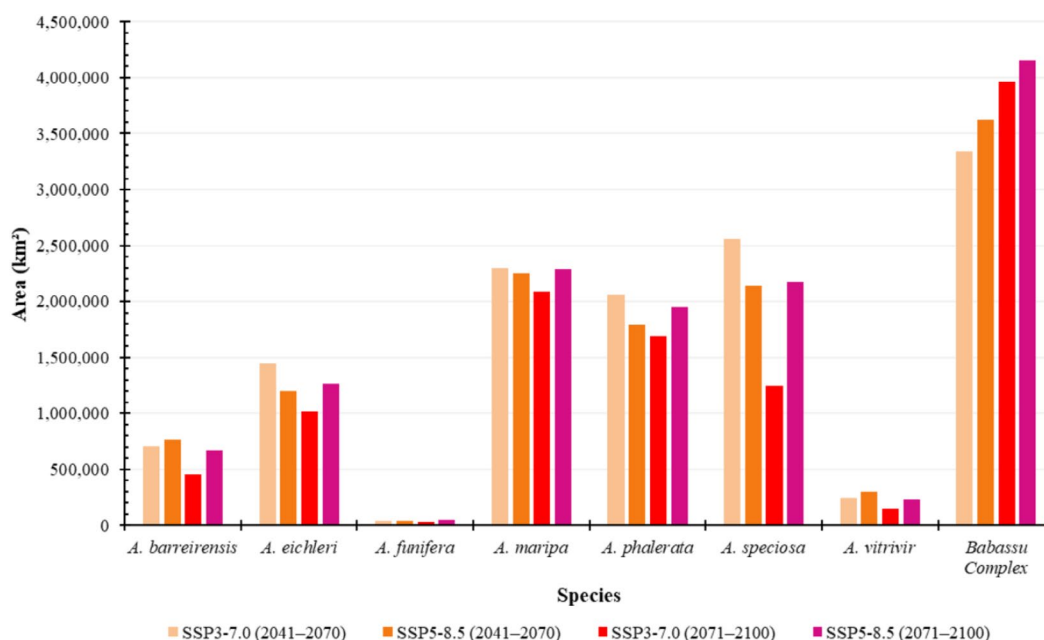


FIGURE 3 | Projected area (km²) of high environmental Suitability for seven *Attalea* species and the Babassu Complex under SSP3-7.0 and SSP5-8.5 scenarios for 2041–2070 and 2071–2100.

generalised more conservatively (Norberg et al. 2019; Valavi et al. 2022). Ensemble models mitigated individual algorithm biases, improving robustness, predictive reliability, and generalisation capacity, particularly when dealing with species that have varied ecological traits and data availability (e.g., widespread generalists like *A. speciosa* vs. narrowly distributed taxa like *A. vitrivir*) (Hao et al. 2019; Kaky et al. 2020; Marmion et al. 2009; Valavi et al. 2022).

It is anticipated that climate change will favour species capable of tolerating warmer and more variable climatic conditions, thereby enhancing their performance and facilitating their spread into new areas (Blois et al. 2013). Projections indicate a potential expansion of bioclimatic suitability for species of the Babassu Complex under future climate scenarios. This expansion could significantly affect savanna ecosystems such as the Brazilian Cerrado and the Venezuelan Llanos, as well as degraded areas of the Amazon rainforest (Santos et al. 2022), potentially altering ecological dynamics and species interactions (Rosenblatt and Schmitz 2014). The presence of highly suitable habitats in these regions may allow babassu species to disperse from adjacent ecosystems and integrate into local communities (Blois et al. 2013; Gehring et al. 2020).

This ecological shift presents both opportunities and risks. On one hand, babassu expansion may support biodiversity restoration and the livelihoods of traditional communities that depend on palm products (Mitja et al. 2019; Porro et al. 2011). On the other, unmanaged expansion could lead to ecological imbalances and potential invasiveness with the potential to reshape local vegetation structure, alter resource availability for other plants and animals, and influence key ecological processes such as fire regimes and competition for space and nutrients (Alves et al. 2019; De Kort et al. 2021; Gehring et al. 2020). This dual nature calls for proactive management strategies that mitigate ecological risks while maximising

socioeconomic and environmental gains through sustainable extractivism, agroforestry integration, and community-led conservation.

Despite potential ecological concerns related to mismanagement, Babassu palms are deeply integrated into the cultural and economic fabric of traditional communities, contributing food, oil, fibre, and income (De Oliveira et al. 2022; Mitja et al. 2019; Porro et al. 2011; Shiraiishi Neto 2017). The projected expansion of climatically suitable areas for babassu species offers practical opportunities for both conservation and sustainable use of its species. Regions such as the Cerrado–Amazon transition zone and the Venezuelan Llanos, where species like *A. speciosa*, *A. maripa*, and *A. phalerata* are projected to expand, should be prioritised for sustainable extractivism and community-based agroforestry initiatives that align with traditional livelihoods and promote biodiversity conservation (Almeida Campos et al. 2015; De Oliveira et al. 2022; Mitja et al. 2019). In contrast, species with more restricted distributions and higher vulnerability to climatic shifts, including *A. vitrivir* and *A. funifera*, demand targeted in situ conservation actions in regions identified as future climatic refugia (Lannuzel et al. 2021; Volis and Tojibaev 2021). Integrating species distribution models with local ecological knowledge and land-use planning offers a pathway for designing resilient socioecological systems that support both biodiversity and human well-being under climate change (Porro et al. 2011; Valavi et al. 2022).

Moreover, while SDMs predict broad future suitability, actual expansion is contingent on factors like dispersal ability, landscape connectivity, and biogeographic barriers. Thus, expansion is not guaranteed and must be interpreted with caution. These results also corroborate Eiserhardt et al. (2011), who emphasised palm species' sensitivity to cold and seasonal climates due to limited frost tolerance and dormancy mechanisms. This physiological sensitivity helps explain the concentration of unsuitable

habitats in arid and colder regions, where thermal stress and low humidity act as constraints on distribution.

Ongoing changes in land use and land cover have already had an impact on the geographic distribution of many species, disrupting taxonomic flows and reducing biodiversity at both present and future scales (Adhikari et al. 2022; Bellard et al. 2012; Trautmann 2018). Given that some babassu species are associated with anthropized landscapes (Gehring et al. 2020; Santos et al. 2022), incorporating anthropogenic variables such as land use, biological interactions, topography, and edaphic conditions into modelling efforts could improve the accuracy of distribution projections (Blach-Overgaard et al. 2010; Frans et al. 2022; Nuñez-Penichet et al. 2024; Silva et al. 2023; Vedel-Sørensen et al. 2013; Zuquim et al. 2023). The resilience of these species to disturbed environments (Santos et al. 2022), coupled with the interaction of ecological and anthropogenic factors, may be key determinants of their persistence and potential expansion under future scenarios.

Moreover, it is imperative to interpret SDM predictions as testable hypotheses rather than as direct substitutes for actual population parameters. To ensure reliability and applicability in ecological planning, it is essential to validate these models when utilising them to guide conservation decisions (Lee-Yaw et al. 2022).

4.1 | Research Limitations

While this study provides valuable insights into the climate-driven distribution shifts of the Babassu Complex, several limitations should be acknowledged. First, the use of a uniform Neotropical background extent for all species, including those with restricted distributions (e.g., *A. funifera*, *A. vitrivir*), may have overestimated suitability for rare taxa by incorporating ecologically irrelevant areas. Future studies could refine predictions by testing species-specific extents based on dispersal constraints or biogeographic barriers (Vasquez et al. 2021; Whitford et al. 2024). Second, anthropogenic factors such as land-use change, habitat fragmentation, and human-mediated dispersal were not incorporated, potentially inflating projected suitability in heavily modified landscapes (Blach-Overgaard et al. 2010; Nuñez-Penichet et al. 2024). Third, the models assume unlimited dispersal, ignoring geographic barriers (e.g., deforestation, mountain ranges) that may limit range shifts (Adhikari et al. 2022; Qiao et al. 2019). Finally, while ensemble modelling mitigated algorithmic biases, field validation is needed to confirm predicted expansions, particularly for species with low occurrence records (Franklin 2023; Lee-Yaw et al. 2022). Addressing these limitations through integrated socio-ecological frameworks will enhance the practical utility of SDMs for conservation planning.

5 | Conclusions

The projected responses of Babassu species to climate change reveal distinct ecological strategies and potential biogeographic shifts. Generalist species such as *A. speciosa*, *A. maripa*, and *A. phalerata* show broad tolerance to warmer and more seasonal

climates, suggesting potential range expansions into transitional and anthropised environments. In contrast, *A. vitrivir* and *A. funifera* show narrow climatic suitability, indicating higher sensibility to climate changes. These patterns underscore the dual role of climate as both a driver of expansion and a constraint on persistence, emphasising the need for species-specific conservation strategies. Beyond mapping distributions, these findings contribute to a broader understanding of how tropical plant species may reorganise in response to shifting climatic envelopes. Such reorganisation has implications not only for local ecosystems and community structure but also for long-distance floristic connectivity, endemism patterns, and the future configuration of Neotropical biotas.

By integrating the strengths of multiple algorithms and mitigating individual model biases, species distribution modelling (SDM) techniques provide robust insights into current and future biogeographic patterns. Within the Babassu Complex, these approaches have helped fill critical knowledge gaps, highlighting how species with different ecological traits and climatic tolerances may respond unevenly to environmental change. While ensemble species distribution models remain powerful tools for anticipating these changes, the key insight lies in their ecological interpretation: predicting not just where species might go, but how they will interact with existing communities and processes when they arrive.

A forward-looking conservation biogeography should therefore combine modelling with field validation and ecological data to better anticipate species responses. Thus, future research should focus on incorporating anthropogenic variables, validating predictions with field data, and exploring species-specific ecological responses to climate change. A multidisciplinary approach that combines species distribution modelling with ecological and socioeconomic assessments will be essential for developing effective conservation and management strategies in the face of ongoing environmental change.

Author Contributions

D.P. Santos was responsible for compiling the database, conducting the modelling procedures, analysing the results, and preparing the figures and tables, under the guidance of the co-authors. All authors contributed to the conceptualisation, writing, and revision of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All species occurrence records are available via GBIF, and bioclimatic variables were sourced from the CHELSA database. The full set of modelling scripts and processed data has been deposited on Zenodo (<https://doi.org/10.5281/zenodo.15265496>), ensuring full transparency and reproducibility of all analyses and results.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jbi70027-sup-0001-Supinfo.docx.